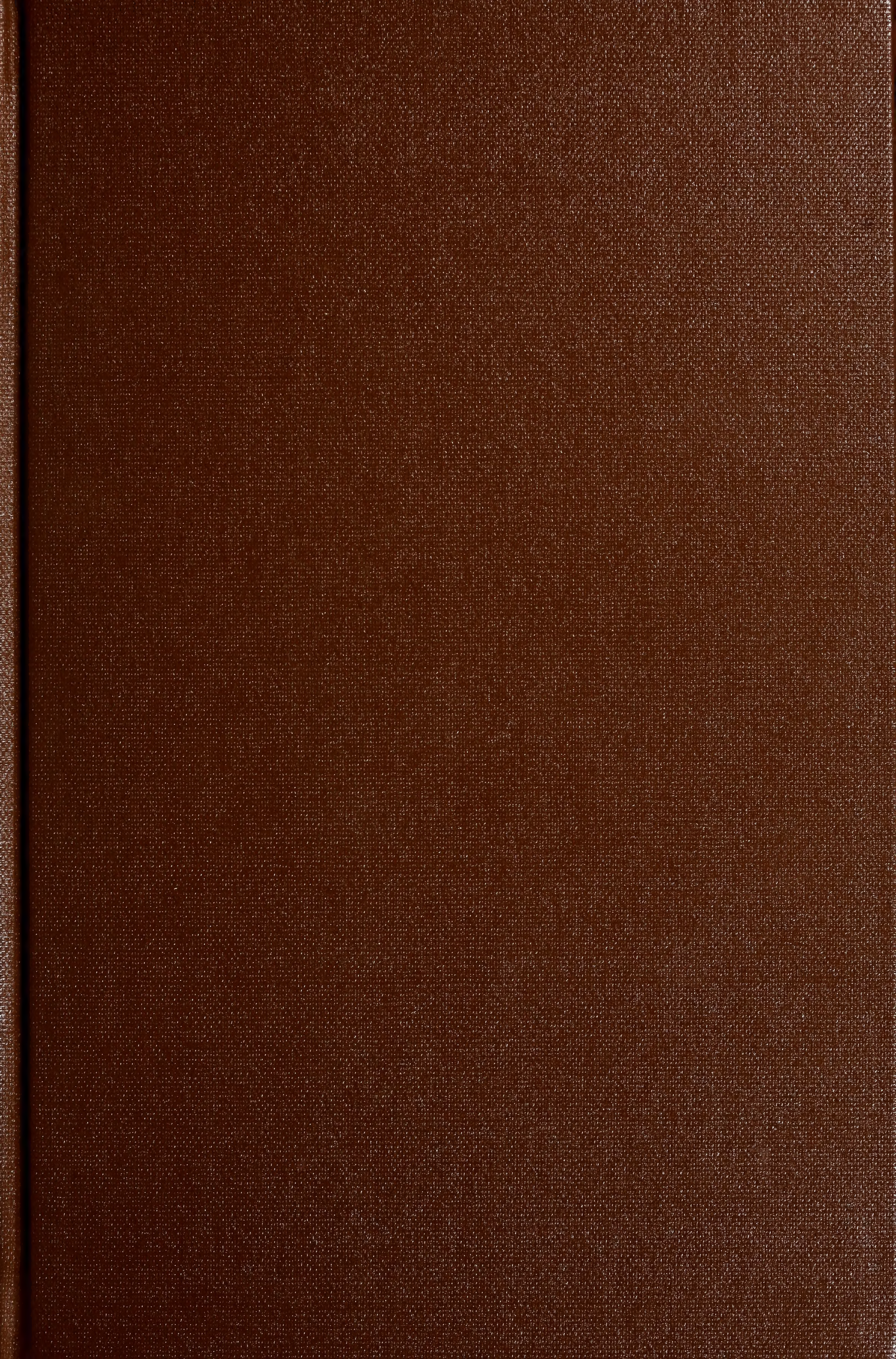
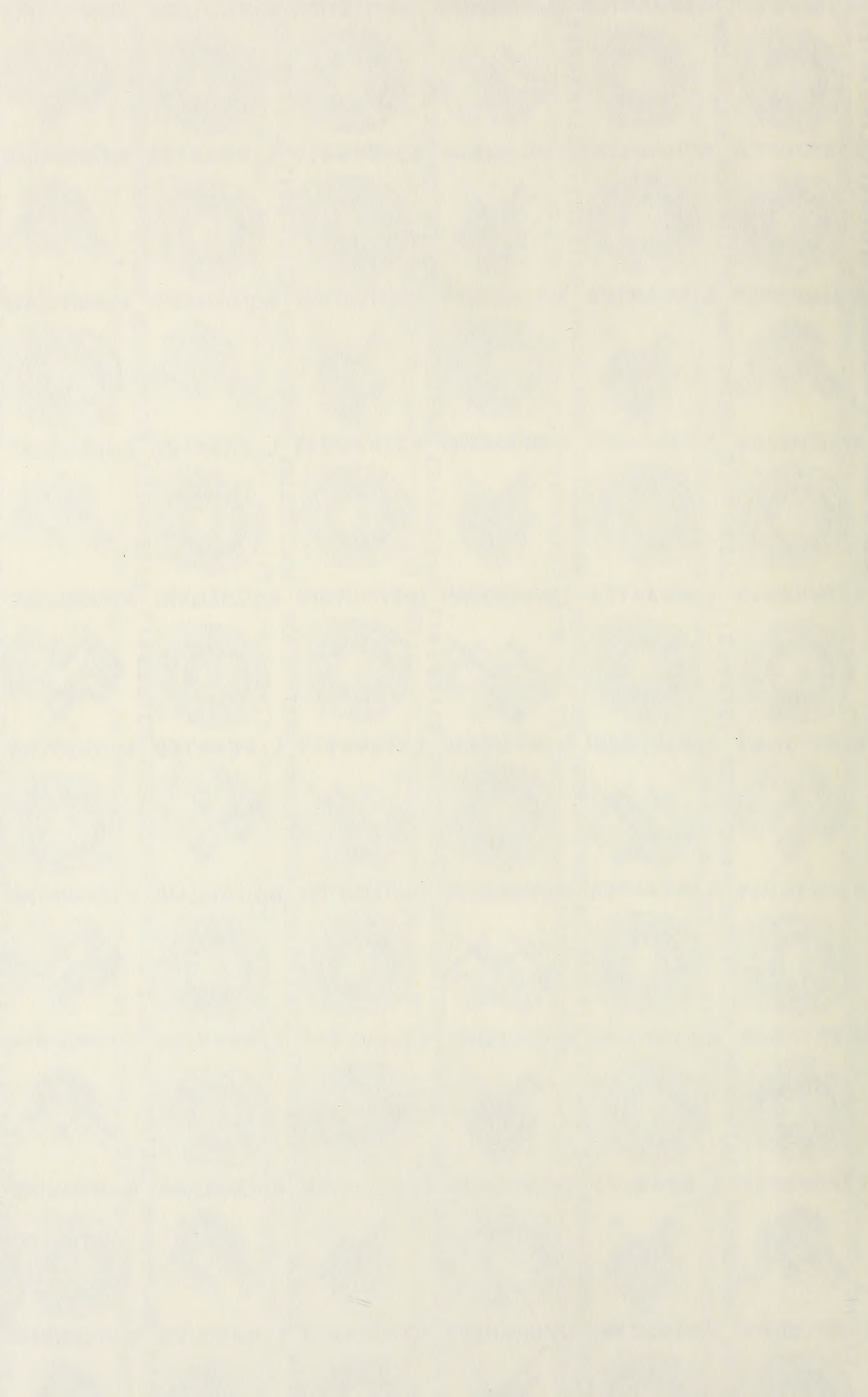








ZEITSCHRIFT FÜR SÄUGETIERKUNDE

INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Organ der Deutschen Gesellschaft für Säugetierkunde

Volume 58, 1993 ISSN 0044-3468

Mit 153 Abbildungen



Verlag Paul Parey Hamburg und Berlin



Wissenschaftliche Originalarbeiten

Wissenschaftliche Kurzmitteilungen

Mitteilungen der Gesellschaft

Buchbesprechungen



This journal is covered by Biosciences Information Service of Biological Abstracts, and by Current Contents (Series Agriculture, Biology, and Environmental Sciences) of Institute for Scientific Information

 Verlag: Paul Parey, Hamburg und Berlin. Anschriften: Spitalerstraße 12, D-20095 Hamburg; Seelbuschring 9–17, D-12105 Berlin, Bundesrepublik Deutschland. Printed in Germany by Westholsteinische Verlagsdruckerei Boyens & Co., Heide/Holstein

ISSN 0044-3468 58 (1–6) 1–384 (1993)



1), 1–64, Februar 1993 ISSN 0044-3468 C 21274 F

ZEITSCHRIFT FÜR SÄUGETIERKUNDE

INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Organ der Deutschen Gesellschaft für Säugetierkunde





Verlag Paul Parey Hamburg und Berlin

This journal is covered by Biosciences Information Service of Biological Abstracts, and by Current Contents (Series Agriculture, Biology, and Environmental Sciences) of Institute for Scientific Information

---

Die Zeitschrift für Säugetierkunde veröffentlicht Originalarbeiten und wissenschaftliche Kurzmitteilungen aus dem Gesamtgebiet der Säugetierkunde, Besprechungen der wichtigsten internationalen Literatur sowie die Bekanntmachungen der Deutschen Gesellschaft für Säugetierkunde. Verantwortlicher Schriftleiter im Sinne des Hamburgischen Pressegesetzes ist Prof. Dr. Dieter Kruska.

Zusätzlich erscheint einmal im Jahr ein Heft mit den Abstracts der Vorträge, die auf der jeweiligen Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde gehalten werden. Sie werden als Supplement dem betreffenden Jahrgang der Zeitschrift zugeordnet. Verantwortlich für ihren Inhalt sind ausschließlich die Autoren der Abstracts.

Manuskripte: Manuskriptsendungen sind zu richten an die Schriftleitung, z. Hd. Prof. Dr. Dieter Kruska, Institut für Haustierkunde, Biologie-Zentrum, Neue Universität, Olshausenstr. 40–60, W-2300 Kiel, Bundesrepublik Deutschland. Für die Publikation vorgesehene Manuskripte sollen gemäß den „Redaktionellen Richtlinien" abgefaßt werden. In ihnen finden sich weitere Hinweise zur Annahme von Manuskripten, Bedingungen für die Veröffentlichung und die Drucklegung, ferner Richtlinien für die Abfassung eines Abstracts und eine Korrekturzeichentabelle. Die Richtlinien sind auf Anfrage bei der Schriftleitung und dem Verlag erhältlich.

Sonderdrucke: Anstelle einer Unkostenvergütung erhalten die Verfasser von Originalbeiträgen und Wissenschaftlichen Kurzmitteilungen 50 unberechnete Sonderdrucke. Mehrbedarf steht gegen Berechnung zur Verfügung, jedoch muß die Bestellung spätestens mit der Rücksendung der Korrekturfahnen erfolgen.

Fortsetzung 3. Umschlagseite

 Verlag: Paul Parey, Hamburg und Berlin. Anschriften: Spitalerstr. 12, D-2000 Hamburg 1; Seelbuschring 9–17, D-1000 Berlin 42, Bundesrepublik Deutschland. – Printed in Germany by Westholsteinische Verlagsdruckerei Boyens & Co., Heide/Holst.

Z. Säugetierkunde 58 (1993) 1–12

ISSN 0044-3468

Fixstreifen-Taxation: Ein Vorschlag für eine neue Schätzmethode von Wasserfledermäusen, *Myotis daubentoni*, im Jagdgebiet

Von I. Rieger und Doris Walzthöny

Fledermaus-Gruppe Rheinfall, Dachsen, Schweiz

Eingang des Ms 31. 3. 1992
Annahme des Ms. 15. 6. 1992

Abstract

A proposition for a new method to estimate the number of hunting Daubenton's bats, Myotis daubentoni

Evaluated several methods that could be used for an estimation for the population density of Daubenton's bats hunting over the rhine. A new estimation method was developed: counting all Daubenton's bats flying through a light beam immediately above water surface running from bank to bank, in a right angle to the river direction. Based on these counts, the number of bats per kilometre of river was calculated. This new estimation method was tested in a computer simulation and its accuracy was estimated.

Einleitung

Im Januar 1989 bat der Naturschutzverein Dachsen (NVD) einen von uns (IR), das Projekt „Fledermaus-Inventar Dachsen“ zu leiten. Ziel dieses Projekts ist unter anderem, den Bestand der Fledermäuse auf dem Gemeindegebiet zu erfassen und zu inventarisieren, damit in kommenden Jahren die Daten ergänzt und Bestandesentwicklungen abgeleitet werden können.

Die Studien von Haffner und Stutz (1985), Müller und Widmer (1985), Stutz (1985) und Rieger et al. (1990) geben eine Übersicht über die in der Umgebung des Rheinfalls lebenden Fledermausarten. Alle Autoren erwähnen, daß Wasserfledermäuse über dem Rhein jagen, aber es werden nur allgemeine Hinweise über Vorkommen, Jagdverhalten und zum Teil über Quartiere gegeben. Quantitative Angaben beschränken sich auf Fledermausquartiere in Gebäuden.

Wasserfledermäuse bewohnen in dieser Region vorwiegend Baumhöhlenquartiere. Wir kennen erst seit kurzem einige wenige dieser Quartiere (Müller 1991), so daß Ausflugszählungen ungenügende Informationen für Bestandesschätzungen erbringen. Ebensowenig eignen sich Zählungen auf den Flugstraßen, weil wir dabei nur einen Teil der Wasserfledermaus-Population erfassen: Wasserfledermäuse nutzen mehr als nur eine Flugstraße, aber nur wenige sind bekannt (Rieger et al. 1990). Dagegen dürfte ein großer Teil der regionalen Wasserfledermaus-Population über dem Rhein jagen. Quantitative Angaben über die Wasserfledermäuse im Jagdgebiet lassen sich für Bestandeskontrollen daher besser verwenden.

Wasserfledermäuse jagen meist wenige Zentimeter bis rund einen Meter über der Oberfläche von stehenden oder langsam fließenden Gewässern (Stutz 1985; Kulzer et al. 1987; Schober und Grimmberger 1987; Kalko und Schnitzler 1989). Um den Bestand der Wasserfledermäuse in ihrem Jagdgebiet abzuschätzen, prüften wir drei Methoden auf ihre Eignung: Luftbildkontrollen, Scheinwerfer-Streifentaxation und die von uns neu entwickelte Fixstreifen-Taxation.

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5801-0001 $ 02.50/0

Material und Methode

Evaluation Luftbildkontrollen

Mit einer Kamera mit Weitwinkelobjektiv, die mindestens 60 Meter über der Wasseroberfläche positioniert und vertikal nach unten gerichtet ist, können jagende Wasserfledermäuse erfaßt werden, wenn zwei Voraussetzungen erfüllt sind: 1. Die Aufzeichnungsmethode registriert einen ausreichenden Kontrast zwischen Fledermaus und Umgebung, in unserem Fall dem Rhein. 2. Man muß die Kamera in die Aufnahmeposition, d.h. mindestens 60 Meter über dem Rhein, bringen. Ein Nachteil bei dieser Anordnung der Kamera wäre, daß Wasserfledermäuse, die in Ufernähe, d.h. unter den überhängenden Ästen der Bäume jagen, kaum in einem Bild mit vertikaler Blickrichtung registriert werden. Bei erfüllten Voraussetzungen könnte man jedoch mit Vertikal-Bildserien zusätzlich Informationen über die Jagdfluggeschwindigkeit und eventuell die Größe des individuellen Jagdgebiets erhalten. Wir klärten die Eignung folgender Technologien ab: militärische Luftüberwachung, Radar/Zielfolge-Radar und Wärmebildgerät.

Militärische Luftüberwachung: Der Leiter der Dienststelle Luftaufklärung der Schweizer Armee teilte uns mit, daß die hier verwendeten Apparate eine zu geringe Auflösung haben, als daß Wasserfledermäuse registriert werden könnten. Zudem macht die Dienststelle Luftaufklärung keine Nachtflüge in der Hauptjagdsaison der Wasserfledermäuse (Hürlimann, schriftl. Mitt.).

Radar: Im Radar werden Wasserfledermäuse kaum aufgelöst, wenn sie nahe über einer Oberfläche (Wasser mit Wellen) und vor einem Hintergrund (Wald) fliegen, die selbst Radar-Echos liefern (Bruderer, mündl. Mitt.).

Wärmebildgerät: Erste Erfahrungen zeigten, daß man mit einem optronischen Beobachtungsgerät (= Wärmebildgerät) über dem Rhein jagende Wasserfledermäuse nur unter günstigen Bedingungen beobachten kann. Systematische Beobachtungen, bei denen das Wärmebildgerät rund 50 bis 80 m über der Wasseroberfläche plaziert und vertikal nach unten, auf die Wasseroberfläche gerichtet ist, sind denkbar aber kaum durchzuführen.

Scheinwerfer-Streifentaxation

Bei der Scheinwerfer-Streifentaxation wird ein eng gebündelter Lichtstrahl über eine Fläche bewegt, beispielsweise aus einem fahrenden Geländeauto heraus. Alle Objekte, die der Lichtstrahl erfaßt, werden gezählt. Diese Methode wird vor allem angewendet bei Bestandesschätzungen von hasen- bis hirschgroßen Wildtieren (Blankenhorn et al. 1978; Pfister 1978). Zu den wichtigsten Bedingungen für eine erfolgreiche Streifentaxation gehören folgende: Die Zählobjekte bewegen sich auf einer Ebene, und das Verhältnis der Fortbewegungsgeschwindigkeiten von Zählstreifen (= Lichtstrahl) zu Zählobjekten: der Zählstreifen muß sich immer rascher bewegen als die Zählobjekte.

Bei äsenden Wildtieren, die in der Dämmerung und nachts von einem fahrenden Geländeauto aus taxiert werden, sind diese Bedingungen in der Regel stets erfüllt.

Bei Wasserfledermäusen ist die erste Bedingung erfüllt; denn die Tiere fliegen in einem engen Luftraum unmittelbar über der Wasseroberfläche, so daß alle Tiere in einem Lichtstrahl über der Wasseroberfläche erfaßt werden. Die zweite Bedingung ist dagegen schwieriger zu erfüllen. Bei unseren Messungen an den Flugstraßen flogen Wasserfledermäuse mit 25 bis 30 km/h (Rieger et al. 1990). Kalko und Schnitzler (1989) erwähnen 12 km/h. Um unter diesen Umständen eine Scheinwerfer-Streifentaxation durchzuführen, müßte ein Boot benutzt werden, welches bis 30 km/h fährt. Bei dieser Geschwindigkeit ist eine Fledermaus, die sich rechtwinklig zur Fahrtrichtung des Bootes bewegt, im 2 m breiten Lichtstrahl 0.36 sec lang zu sehen. Wenn sich die Fledermaus in der zum Boot entgegengesetzten Richtung bewegt, wird sie nur noch während 0.18 sec erfaßt. Eine beachtliche Zählungenauigkeit ist zu erwarten. Wir verwarfen daher den Gedanken, den Bestand der über dem Rhein jagenden Wasserfledermäuse mit dieser Methode zu schätzen.

Fixstreifen-Taxation, eine neue Methode

Die Überlegungen zur Scheinwerfer-Streifentaxation führten zu einer neuen Schätzmethode, die wir Fixstreifen-Taxation nennen. Dabei kann mit relativ geringem Aufwand in folgender Weise verfahren werden: Ein eng gebündelter Lichtstrahl sollte vom Flußufer aus in rechtem Winkel zur Fließrichtung unmittelbar über dem Wasserspiegel plaziert werden, um einen Ausschnitt des Jagdgebiets der Wasserfledermäuse zu beleuchten. Alle Wasserfledermäuse, die im Lichtstrahl erscheinen, können dann gezählt werden. Weiterhin ist zu ermitteln, in wie vielen Zeiteinheiten wie viele Wasserfledermäuse im Lichtstrahl erfaßt werden.

Bei dieser Methode gehen wir davon aus, daß eine einfache Korrelation besteht zwischen der Anzahl über dem Rhein jagender Wasserfledermäuse und der Anzahl von Wasserfledermäusen, die im Lichtstrahl erscheinen. Wir entwarfen das Computerprogramm MOVETAX, welches die Ausgangslage und die anvisierte Zählmethode simuliert, um folgende Fragen zu beantworten:

1. Wie ist die Anzahl von Tieren, die in einem Zählstreifen erscheinen, mit der Anzahl von Tieren korreliert, die innerhalb einer bestimmten Fläche jagen?
2. Wie lange muß gezählt werden, um eine optimale Schätzgenauigkeit zu erreichen?

Für die Schätzung des jagenden Wasserfledermaus-Bestandes über dem Rhein programmierten wir die Computer-Simulation MOVETAX mit Hilfe der Programmiersprache Turbo Pascal (Borland 1987). Die Simulationen rechneten wir auf einem IBM-kompatiblen Personal-Computer.

Für die Zählungen benutzten wir einen Akku-betriebenen Scheinwerfer (vom Albis-Nachtsichtgerät ARGUS, Einsatz mit Weißlicht), eine Stoppuhr und einen Fledermaus-Detektor. In der Jagdsaison 1990 zählten wir jeweils zu Beginn der nächtlichen Jagdaktivität am Beobachtungspunkt ZD001 (Koordinaten 688.000 / 288.050). Wir begannen unsere Beobachtungen rund 15 Minuten nach dem astronomischen Sonnenuntergang, d. h. bevor die erste Wasserfledermaus festgestellt werden konnte. Die erste Zählphase begann, nachdem wir die erste Wasserfledermaus im Jagdgebiet beobachteten. Wir beendeten eine Zählphase nach 2 bis 3 Minuten. Pro Beobachtungsabend führten wir 8 Zählphasen durch, je im Abstand von 5 Minuten.

Neben qualitativen Parametern wie Bewölkung (synoptische Skala von 0 bis 8), Wind (Beaufortskala von 1 bis 12), Temperatur (°C), Insekten-Angebot (subjektive Skala von 1 [= keine] bis 4 [= sehr viele]) notierten wir von jeder Zählphase Dauer (sec), Anzahl Wasserfledermäuse im Lichtstrahl (n) und Zählphasenende (Uhrzeit).

Die Computer-Simulation MOVETAX

Das Programm MOVETAX simuliert folgende Parameter:

„Jagdgebiet" der Wasserfledermäuse (Abb. 1). Da die Simulation nicht nur ein rechnerischer Prozeß ist, sondern jeder simulierte Zustand auf dem PC-Bildschirm auch dargestellt werden soll, ist das „Jagdgebiet" in seiner Ausdehnung limitiert (wenn wir mit Realbegriffen Bezug auf Vorgänge auf dem PC-Bildschirm nehmen, dann setzten wir diese Bezeichnungen in Anführungszeichen).

FBR: Die Breite des „Jagdgebiets" oder „Flußbreite" kann zwischen 2 und 23 Distanz-Einheiten betragen.
UL: Die Länge des „Jagdgebiets" beträgt 79 Distanz-Einheiten.

Zählstreifen (= Lichtstrahl). Der Zählstreifen verläuft rechtwinklig zum „Ufer" des „Jagdgebiets". Er ist eine Distanz-Einheit breit. Das Programm MOVETAX legt den Zählstreifen zu Beginn jeder neuen Simulation an einer zufällig ausgewählten Position über das „Jagdgebiet".

Fortbewegung jagender Wasserfledermäuse. Die Fortbewegung der „Wasserfledermäuse" setzt sich zusammen aus den Komponenten Geschwindigkeit und Richtung.

FG: Fluggeschwindigkeit entspricht 1 (Distanz-Einheit/Zeit-Einheit). In der Simulation ist die Fluggeschwindigkeit konstant: pro Zeit-Einheit bewegt sich jedes „Tier" im Testfeld um eine Distanz-Einheit fort.
R: Richtung. Ein Zufallsgenerator bestimmt die Fortbewegungsrichtung. Es stehen acht Fortbewegungsrichtungen zur Auswahl: N, S, W, E, NW, SW, NE, SE. Wenn die Fortbewegungsrichtung das „Tier" über das „Ufer", d. h. den N- oder S-Rand des Testfeldes bringen

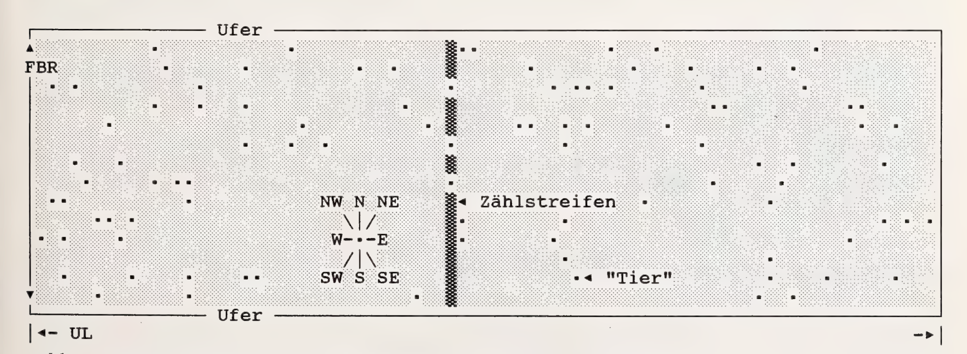


Abb. 1. Beispiel eines Simulationszustandes: Die Computer-Simulation MOVETAX stellt das Jagdgebiet als Rechteck (FBR × UL) dar, setzt TAE „Tiere" (■) zufällig in dieses Rechteck, legt einen Zählstreifen parallel zur Rechteck-Breite, bewegt alle „Tiere" zufällig und zählt alle „Tiere", die im Zählstreifen erscheinen

würde, wird nur die W-E-Komponente der Fortbewegung ausgeführt. Wenn das „Tier“ den W- oder E-Rand des Testfeldes überfliegt, erscheint es wieder am gegenüberliegenden Ende des Testfeldes.

Weitere Parameter:

TAE: Anzahl eingesetzter „Tiere“. Die Größe des Testfeldes beschränkt die maximale Anzahl der eingesetzten „Tiere“. Lediglich aus ästhetischen Gründen akzeptiert MOVETAX höchstens ein Drittel so viele „Tiere“ wie das „Jagdgebiet“ Distanz-Einheits-Rechtecke (FBR × UL) hat.

ABB: Abbruchbedingung. MOVETAX stoppt die Simulation, wenn es ABB „Tiere“ im Zählstreifen (siehe unten TZG) erfaßt hat.

WHP: Wiederholungen. Mit diesem Parameter legen wir fest, wie viele Simulationen das Programm mit identischen Parametern rechnen muß.

SGE: Simulationsgeschwindigkeit. Mit diesem Parameter reduzieren wir die Simulationsgeschwindigkeit so weit, daß wir die simulierten Verhaltensweisen mit dem Auge erfassen und die dargestellten Abläufe beurteilen können.

Das Computer-Simulation MOVETAX berechnet aus den eingegebenen Parametern die folgenden Werte:

TDE: Soll-„Tier“-Dichte (Distanz-Einheit^{-1}). Aus der Anzahl eingesetzter „Tiere“ TAE und der „Ufer“-Länge UL berechnet das Programm die Dichte der „Tiere“ pro „Ufer“-Längen-Distanz-Einheit.

$$TDE = TAE / UL \qquad (1)$$

Wir prüfen mit Hilfe der Computer-Simulation MOVETAX eine Schätzmethode und Berechnungsformel, welche als Resultat diesen Wert TDE ergibt.

TZG: Im Zählstreifen erfaßte „Tiere“ (n). Nach jeder Zeit-Einheit erfaßt das Programm alle „Tiere“, die sich im „Zählstreifen“ aufhalten und summiert diese Zahl zur Summe der bis dahin erfaßten „Tiere“.

SZE: Simulationsdauer (Zeiteinheit). Zeitdauer, während der das Programm „Tiere“ im Zählstreifen erfaßt und aufsummiert.

TDS: Simulierte „Tier“-Dichte (Distanz-Einheit^{-1}).

Nach Abbruch der Simulation (entweder nach Erreichen des Abbruchkriteriums ABB oder nach Unterbrechung der Simulation durch den Benutzer) berechnet das Programm die Anzahl „Tiere“ pro Ufer-Längen-Distanz-Einheit. Die entscheidende Überlegung hierzu ist folgende: Wenn in SZE Zeiteinheiten TZG „Tiere“, die sich mit einer konstanten Geschwindigkeit FG fortbewegen, im unbeweglichen Zählstreifen erfaßt werden, dann läßt sich der gleiche Wert auch errechnen, wenn man davon ausginge, daß sich die „Tiere“ nicht bewegen, dafür der Zählstreifen mit der gleichen konstanten Geschwindigkeit FG während SZE Zeiteinheiten parallel zum Ufer fortbewegt und dabei TZG Tiere erfaßt.

Das Programm berechnet den Wert Simulierte „Tier“-Dichte = „Tiere“ pro Distanzeinheit TDS aufgrund dieser Überlegung wie folgt:

$$TDS = TZG / (SZE \times FG) \qquad (2)$$

RSD: Relative Standardabweichung (= Variationskoeffizient). Nach Wallis und Roberts (1960) berechnen wir die relative Standardabweichung als Prozent-Wert der Standardabweichung SD pro TDS.
RSD = (SD von TDS aus WHP Simulationen / Mittel von TDS aus WHP Simulationen) × 100
Die relative Standardabweichung RSD ist ein Maß für die Zähl-Genauigkeit relativ zur berechneten mittleren TDS. Mit einer Wahrscheinlichkeit von 95 % liegt der Schätzwert innerhalb des Bereichs TDS − TDS × RSD ... TDS + TDS × RSD.

KFR: Korrekturfaktor. Sollte sich bei den Überlegungen, die zum Wert TDS führen, ein systematischer Fehler eingeschlichen haben, dann ließe sich dieser mit einem Korrekturfaktor KFR beheben. KFR multipliziert mit dem Wert TDS ergibt TDE:

$$TDE = TDS \times KFR \qquad (3)$$

Aus dieser Formel (3) ergibt sich für die Berechnung des Korrekturfaktors KFR folgende Formel:

$$KFR = TDE / TDS \qquad (4)$$

Programm-„Fehler“

Ein „Tier“, welches sich in aufeinanderfolgenden Zeitzyklen innerhalb des Zählstreifens bewegt, wird nach jedem Zeitzyklus erneut gezählt. Derartige Mehrfachzählungen sind nicht auszuschließen, verlangsamte Simulationen (Parameter SGE) ergaben jedoch, daß diese Fehler gering sind.

Ergebnisse

Vergleich Computer-Simulation mit Fixstreifen-Taxation im Jagdgebiet

Wir nehmen an, daß wir mit der Fixstreifen-Taxation während einer Zählphase am Rhein einige Wasserfledermaus-Individuen mehrmals, andere dagegen nie im Lichtstrahl erfassen. Das gleiche geschieht auch in der Computer-Simulation.

Es ergaben sich ferner keine eindeutigen Reaktionen der Wasserfledermäuse auf den Lichtstrahl: weder mieden noch bevorzugten sie den Lichtbereich. Um zu diesem Aspekt genauere Aussagen machen zu können, müßte man parallel zur Fixstreifen-Taxation Luftbild-Kontrollen durchführen. Erste Tests mit einem optronischen Beobachtungsgerät zeigten, daß jagende Wasserfledermäuse nicht auf den Lichtstrahl reagierten. Bei solchen Tests könnte auch abgeklärt werden, ob jagende Wasserfledermäuse über dem Rhein zufällige (wie in MOVETAX simuliert) oder bevorzugte Flugrichtungen haben.

Genauigkeit

Das Simulationsprogramm MOVETAX akzeptiert Parameter, die zusammen mit nicht veränderbaren Programm-Eigenschaften die Wirklichkeit, d. h. das Fortbewegungsverhalten von Wasserfledermäusen über dem Rhein möglichst gut simulieren sollen. Die Parameter, so vermuten wir, beeinflussen die Schätzgenauigkeit der Fixstreifen-Taxation sowohl in der Simulation als auch in der Wirklichkeit. Mit der Simulation wollen wir Auskunft über die Genauigkeit der Fixstreifen-Taxation erhalten.

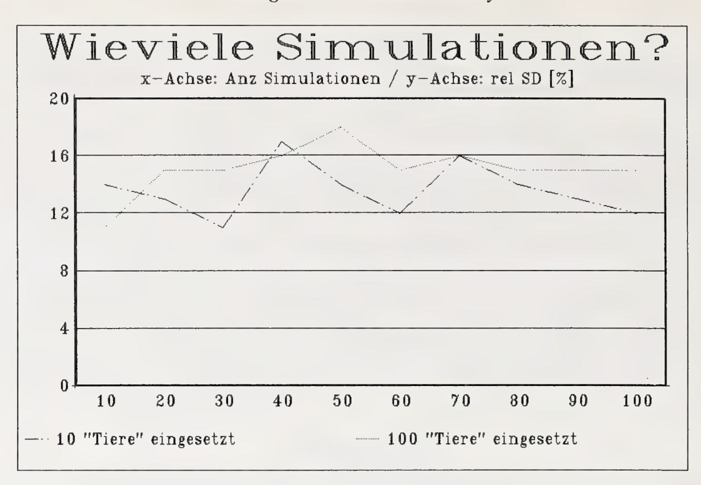
Die variablen Parameter von MOVETAX sind: TAE, FBR und TZG, zusammen mit SZE.

Diese Parameter beeinflussen die Schätzung in einer Weise, die wir nicht mit einer einfachen mathematischen Formel beschreiben können. Mit Hilfe der Computer-Simulation MOVETAX beschreiben wir die Einflüsse dieser Parameter und leiten daraus optimale Bedingungen für die Schätzung des Bestandes über dem Rhein jagender Wasserfledermäuse ab.

Wieviele Simulationen sind nötig mit den gleichen Parametern?

Schon wenige Simulationen mit identischen Parametern zeigen, daß die berechneten Werte TDS von Simulation zu Simulation beträchtlich schwanken können. In einem ersten Schritt bestimmten wir daher, nach wie vielen Simulationen mit identischen Parameterwerten die relativen Standardabweichungen RSD der simulierten „Tier"-Dichte TZG und der Korrekturfaktor KFR sich asymptotisch einem Endwert nähern. Wir ließen das Simulationsprogramm MOVETAX zwei extreme Parameter-Sets je 100mal rechnen. In jeder Simulation mußte das Programm so lange zählen, bis es 1000 Tiere im Zählstreifen (TZG) erfaßt hatte. Im ersten Parameter-Set setzten wir nur 10 „Tiere" auf einen „Fluß" mit „Breite" 2, im zweiten 100 „Tiere" auf einem „Fluß" mit „Breite" 23. Von beiden Parametersets berechneten wir nach 10, 20, 30, 40, 50, 60, 70, 80, 90 und 100 Simulationen Mittelwert, Standardabweichung, Varianz, relative Standardabweichung RSD der „Tier"-Dichte TDS und den Korrekturfaktor KFR (Abb. 2).

Die Kurven in Abb. 2a und b zeigen, daß nach rund 30 bis 50 Simulationen mit gleichem Parameterset die relativen Standardabweichungen RSD und die Korrekturfaktoren KFR konstant bleiben. Mehr als 50 Simulationen ergeben folglich keine größere Genauigkeit. Aufgrund dieser Erkenntnisse verwenden wir für alle weiteren Untersuchungen jeweils die Mittelwerte der „Tier"-Dichten aus 50 Simulationen.



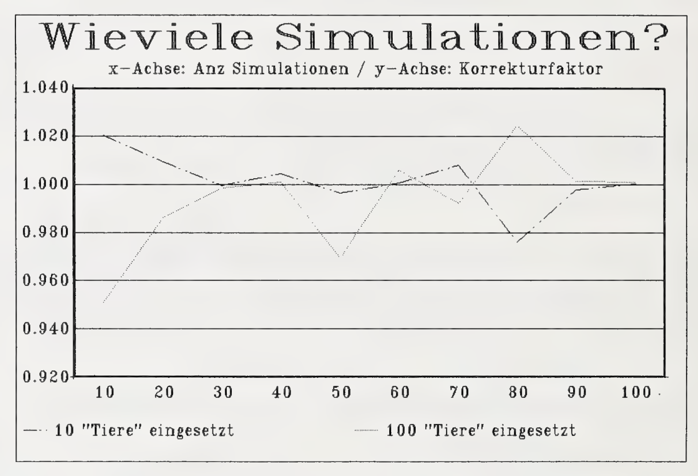


Abb. 2. Die relativen Standardabweichungen RSD (a) und die Korrekturfaktoren KFR (b) erreichen nach rund 30 Simulationen asymptotisch den Endwert. Die Werte bei den Simulationen mit nur 10 „Tieren" im „Jagdgebiet" schwanken viel mehr als jene mit 100 „Tieren" im „Jagdgebiet"

Einfluß der „Flußbreite" FBR

Die „Flußbreite" FBR beeinflußt vor allem die Häufigkeit der Fortbewegungsrichtungen. Bei schmalen „Flüssen" sind Fortbewegungsrichtungen parallel zur „Fließrichtung", der W-E-Richtung, häufiger als quer dazu in N-S-Richtung (Abb. 3). Erst bei großen „Flußbreiten" ist der Einfluß des „Ufers" auf die zufällige Fortbewegungsrichtung der „Tiere" zu vernachlässigen.

Wir führten daher Simulationen mit verschiedenen „Flußbreiten" FBR durch, um den Einfluß dieses Parameters auf die relative Standardabweichung RSD der „Tier"-Dichte TDS und den Korrekturfaktor KFR zu bestimmen. Wir ließen das Programm MOVETAX die simulierten „Tier"-Dichten TDS und Korrekturfaktoren KFR für „Flußbreiten" FBR von 2, 5, 10, 15, 20 und 23 Distanzeinheiten berechnen. Wir setzten in jeder Simulation 100 „Tiere" ein (TAE; 50 „Tiere" bei „Flußbreite"2), ließen das Programm je 10, 100, resp. 500 „Tiere" zählen (TZG) und berechneten die „Tier"-Dichte je Ufer-Längen-Distanz-Einheit aus je 50 Simulationen mit den gleichen Parametern (WHP).

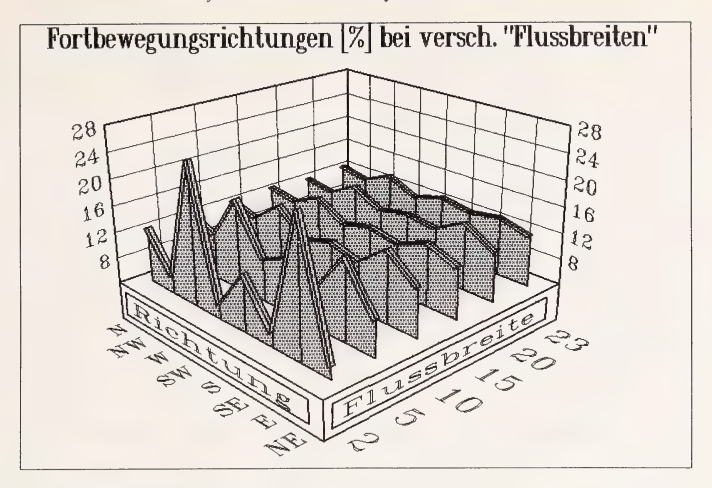


Abb. 3. Aufgrund des Algorithmus der Simulation haben „Tiere", die sich am „N- oder S-Ufer" des „Flusses" aufhalten, eine eingeschränkte Auswahl an Fortbewegungsrichtungen, denn sie können das „Ufer" nicht überfliegen. Bei kleiner „Flußbreite" sind nicht alle 8 möglichen Fortbewegungsrichtungen gleich häufig

Die Resultate dieser Simulationsreihen (Abb. 4a, b) zeigen, daß die „Flußbreite" die Zählmethode nicht beeinflußt. Bei einem gegebenen Parameterset verlaufen die Kurven der relativen Standardabweichungen RSD horizontal, jene der Korrekturfaktoren KFR verlaufen nahe bei 1. Bei einer langen Zählung (bis 500 „Tiere" im Zählstreifen) ist die relative Standardabweichung RSD kleiner (etwa 15 bis 20 %) als bei einer kürzeren (100 „Tiere" im Zählstreifen, etwa 25 bis 30 %). Bei einer sehr kurzen Zählung (Abbruch nach 10 „Tieren" im Zählstreifen) ist die relative Standardabweichung zwischen 50 und 70 % und der Korrekturfaktor deutlich größer als 1.

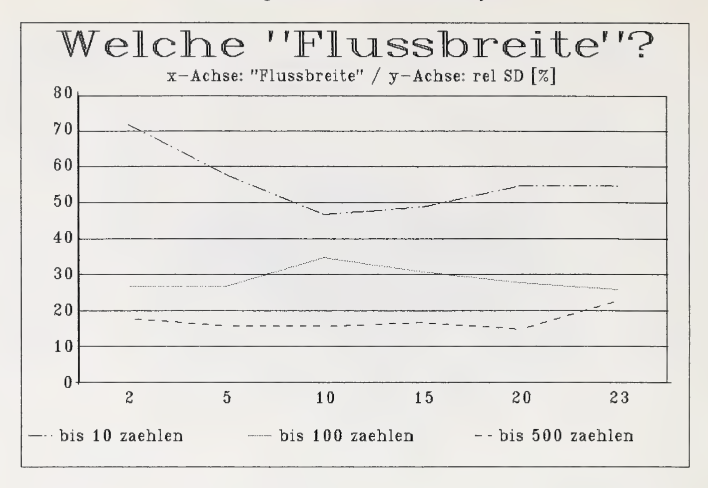
Wie viele „Tiere" muß man zählen, um welche Genauigkeit zu erhalten?

In einem weiteren Testschritt gingen wir der Frage nach, wie sich die Anzahl gezählter „Tiere" auf die Schätzgenauigkeit auswirkt. Dazu ließen wir MOVETAX bei konstanter „Flußbreite" FBR (= 23) und „Tier"-Dichten TAE zwischen 10 und 200 die relativen Standardabweichungen RSD und die Korrekturfaktoren KFR berechnen, wenn es zwischen 5 und 1000 „Tiere" im Zählstreifen zählte.

Bei einer geringen „Tier"-Dichte (10 „Tiere" im „Jagdgebiet" eingesetzt) erreicht die Kurve der relativen Standardabweichungen RSD erst bei 500 bis 750 gezählten „Tieren" einen mehr oder weniger konstanten Wert, bei einer hohen „Tier"-Dichte (200 „Tiere" eingesetzt) erreicht die Kurve der relativen Standardabweichungen RSD schon bei 100 gezählten „Tieren" einen mehr oder weniger konstanten Wert (Abb. 5a). Die Korrekturfaktoren KRF erreichen bei 50 gezählten „Tieren" TZG den Wert 1 (Abb. 5b).

Erkenntnisse aus der Computer-Simulation

MOVETAX berechnet die „Tier"-Dichte pro Ufer-Längen-Distanz-Einheit nach der Formel 2. Der so errechnete Wert TDS stimmt mit dem erwarteten Wert TDE überein und der Korrekturfaktor KFR liegt bei 1 (Formel 3). Das bedeutet, daß man mit der Formel 2



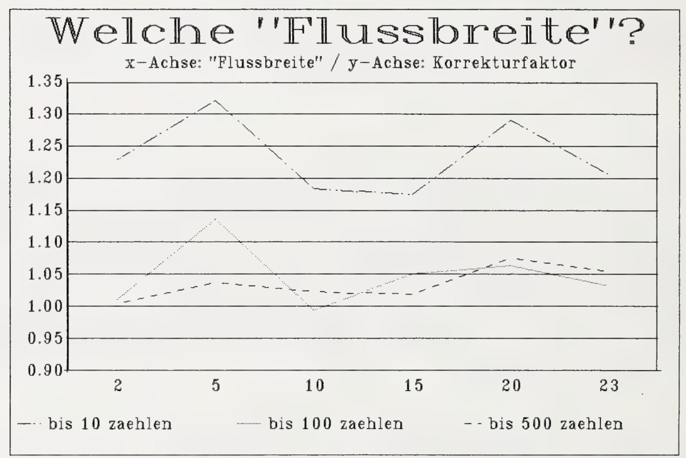
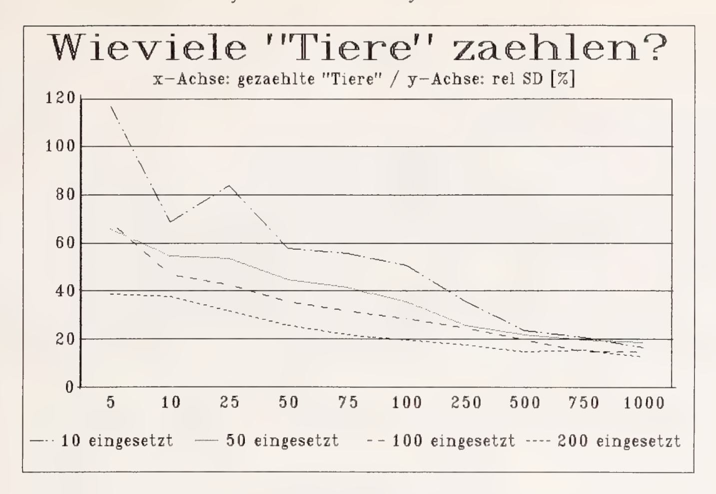


Abb. 4. Bei verschiedenen „Flußbreiten“ verlaufen die Kurven der relativen Standardabweichungen RSD (a) und der Korrekturfaktoren KFR (b) horizontal. Das bedeutet, daß die „Flußbreite“ die Genauigkeit der Simulation nicht beeinflußt. Deutlich zeigen die Kurven, daß die Anzahl gezählter „Tiere“ die Genauigkeit des Resultats beeinflußt: Wenn eine Zählung nach nur 10 im Zählstreifen erfaßter „Tiere“ beendet wird, ergibt dies eine relative Standardabweichung von 50 bis 70 % und einem Korrekturfaktor deutlich neben 1. Wenn man dagegen bis 100 oder gar 500 „Tiere“ im Zählstreifen erfaßt sind, zählt, erreichen die Korrekturfaktoren 1 und die relativen Standardabweichungen sind um 30, resp. um 15 %

aus der Anzahl im Zählstreifen erfaßter „Tiere“ TZG den Bestand im „Jagdgebiet“ berechnen kann.

Die Schätzgenauigkeit, gemessen mit der relativen Standardabweichung RSD, hängt direkt mit der Anzahl gezählter „Tiere“ zusammen. Wir erhalten eine maximale Zähl-Genauigkeit unabhängig von der absolut vorhandenen Anzahl „Tiere“ TAE, wenn wir wenigstens 750 „Tiere“ zählten. Die Genauigkeit liegt in diesem Fall bei 15 bis 20 % relativer Standardabweichung (Abb. 5a).

Bei unseren Beobachtungen am Rhein zählten wir pro Zählphase zwischen 5 und 250 Individuen. Aus Abb. 5a lassen sich die zugehörigen Schätzgenauigkeiten ablesen. Die Fixstreifen-Taxation führt im besten Fall zu Schätzgenauigkeiten von 15 %.



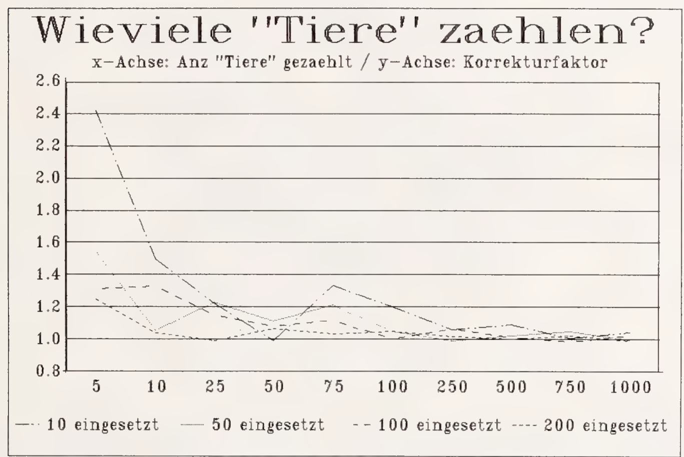


Abb. 5. Die Kurven der Korrekturfaktoren KFR (b) zeigen, daß man wenigstens 50 „Tiere" zählen muß, damit die Korrekturfaktoren bei allen absoluten Tier-Beständen (TAE) nahe bei 1 sind. Die Kurven der relativen Standardabweichungen RSD (c) zeigen, daß mit zunehmender Zähldauer (und Anzahl im Zählstreifen erfaßter „Tiere" TZG) die relativen Standardabweichungen RSD kleiner und damit die Schätzgenauigkeiten größer werden

Die „Flußbreite" beeinflußt weder die Schätzgenauigkeit noch den Korrekturfaktor KFR. Der Korrekturfaktor ist immer nahe bei 1.

Die Feldarbeit – Beobachten und Zählen am Rhein

Allgemeine Beobachtungen

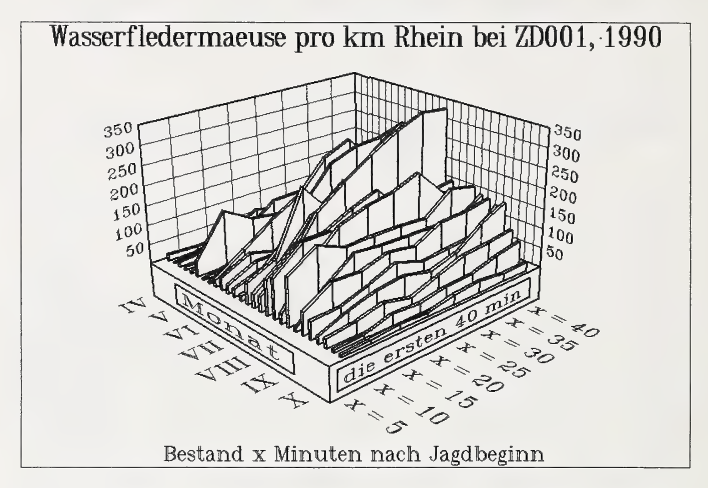
In den ersten rund 15 Minuten, nachdem die erste Wasserfledermaus auf dem Detektor gehört und im Lichtstrahl auch gesehen wurde, jagten die Wasserfledermäuse vorwiegend in Ufernähe, später mehr über dem offenen Wasser. Parallel dazu beobachteten wir Veränderungen in der Verteilung der Insekten über dem Wasser: zuerst waren die meisten unter und nahe bei den Bäumen am Ufer, später flogen sie mehr über der offenen Wasserfläche.

Schätzung des Bestandes jagender Wasserfledermäuse

Unsere Beobachtungen rechneten wir um in Anzahl Wasserfledermäuse pro Kilometer Flußlänge in Anlehnung an Formel (2):

$$\text{Wasserfledermäuse (km}^{-1}) = \frac{\text{Tiere pro Zählphase (sec}^{-1}) \times 3600 \text{ (sec)}}{\text{Dauer Zählphase [sec]} \times \text{Gescwindigkeit (km/h)}} \quad (5)$$

Abb. 6 zeigt die Resultate unserer Beobachtungen aus dem Jahr 1990. Wenn wir als Geschwindigkeit jagender Wasserfledermäuse 12 km/h einsetzen (Kalko und Schnitzler 1990), dann erhalten wir im Hochsommer einen Höchstbestand von rund 300 Tieren pro km Flußlänge. Gegen Ende der 40minütigen Beobachtungsphase erreichen die Bestandeskurven das Maximum. Abb. 6 zeigt, welche Resultate mit der Fixstreifen-Taxation möglich sind.



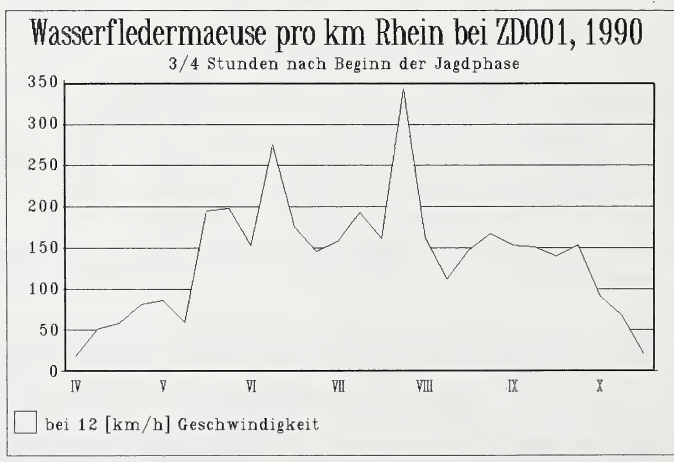


Abb. 6. a: Resultate unserer 1990er Beobachtungen, umgerechnet mit 12 (km/h) Geschwindigkeit. Zwischen der 14. und 40. Woche (April bis Oktober) beobachten wir Wasserfledermäuse über dem Rhein unterhalb des Rheinfalls. In den ersten 40 Minuten nach Beginn der Jagdphase erreichen die Bestandeskurven ein Maximum. b: Auszug aus Abb. 6a: Bestand der letzten (8.) Zählphase jedes Beobachtungstages. Zwei Bestandesmaxima Anfang Juni und Ende Juli fallen auf

Diskussion

Die Computer-Simulation MOVETAX zeigt, daß die grundsätzliche Überlegung richtig ist, wonach aus der Anzahl Tiere, die in einem eng gebündelten Lichtstrahl erfaßt werden, die Tier-Dichte abgeleitet werden kann. Die Simulation zeigt auch, daß wir mit der hier vorgestellten Fixstreifen-Taxation den Bestand von Wasserfledermäusen, die über einem Fließgewässer jagen, innerhalb einer gewissen „methodischen Unschärfe" schätzen können. Bei großer Bestandesdichte und mehr als 500 Tieren im Lichtstrahl, erreicht man Schätzgenauigkeiten zwischen 15 und 20 %.

Die Dichte von Wasserfledermäusen im Jagdgebiet ist nur zu berechnen, wenn ihre Fluggeschwindigkeit bekannt ist. Vorläufig verfügen wir über zu wenig einschlägige Meßwerte. Solange wir keine umfangreichen Messungen der Fluggeschwindigkeit von Wasserfledermäusen im Jagdgebiet haben, arbeiten wir mit der Anzahl Wasserfledermäuse, die pro Zeiteinheit im Lichtstrahl erscheinen. Die Ordinaten-Einteilung in Abb. 6 müßte dann (nach Formel 5 durch den Wert 5 dividiert werden, wenn man die Einheit (Anzahl Wasserfledermäuse pro Minute) verwendet.

Wir vermuten, daß zwischen der Anzahl der Insekten und der Anzahl jagender Fledermäuse eine direkte Korrelation besteht. Es scheint, daß der Beginn der Wasserfledermaus-Jagdphase mit dem Auftreten einer größeren Anzahl von Insekten zusammenfällt.

Während der gesamten Beobachtungszeit führte der Rhein am Beobachtungsort oft Schaumkronen mit sich. Wir hatten den Eindruck, daß über den Flußpartien mit viel Schaum kaum Insekten flogen. Auf jeden Fall aber registrierten wir über den Schaumpartien weniger jagende Wasserfledermäuse als über der schaumfreien Flußoberfläche. Diese Beobachtungen fordern gezieltere Untersuchungen über die Verteilung der Beute der Wasserfledermäuse. Die Hinweise, wonach die Folgen der Gewässerverschmutzung (Schaumbildung) einen direkten Einfluß auf das Jagdverhalten der Wasserfledermäuse haben, verdienen besondere Beachtung.

Danksagung

Die engagierten NVD-Vorstandsmitglieder Thomas Lendenmann, Ruedi Schneider und Jürg Merki halfen uns bei der Planung und Durchführung des Projekts, insbesondere auch bei den koordinierten Fledermausbeobachtungen. Andreas Müller und Hansueli Alder standen uns bei unserer Arbeit am Fledermaus-Inventar mit Rat und Tat zur Seite. Die Grenzwacht Schaffhausen (Herr K. Meier) lieh uns für unsere Untersuchungen ein ARGUS-Nachtsichtgerät. Die Gruppe für Rüstungsdienste, Bern, stellte uns 1991 und 1992 während einer, resp. drei Wochen ein optronisches Beobachtungsgerät (Wärmebildgerät) zur Verfügung. Die Baupläne für Fledermausdetektoren stellten uns Marianne Haffner und Hans-Peter B. Stutz von der Fledermauskoordinationsstelle Ost, Zürich, zur Verfügung. Wir danken allen für ihre Hilfe und Unterstützung.

Zusammenfassung

In der Region Rheinfall jagen viele Wasserfledermäuse über dem Rhein. Wir evaluierten verschiedene Methoden, mit denen der Bestand über dem Rhein jagender Wasserfledermäuse geschätzt werden könnte und entwickelten eine neue Schätzmethode: wir zählten alle Wasserfledermäuse, die durch einen Lichtstrahl über dem Fluß quer zur Flußrichtung flogen und berechneten daraus die Anzahl Tiere pro km Flußlänge. Mit Hilfe einer Computer-Simulation prüften wir diese neue Methode und bestimmten ihre Genauigkeit.

Literatur

Borland (1987): Turbo Pascal Reference Guide Version 5.0. Scotts Valley: Borland Int.

Blankenhorn, H. J.; Müller, H. U.; Buchli, Ch. (1978): Scheinwerfertaxation von Hirsch- und Rehbeständen. Wildbiologie für die Praxis **3** (1), 1–6.

Haffner, M.; Stutz, H. P. (1985): Geschlechtsspezifische saisonale Anwesenheit einiger mitteleuropäischser Fledermausarten in der Zentral- und Ostschweiz. Mitt. natf. Ges. Schaffhausen **32**, 209–213.

Kalko, E. K. V.; Schnitzler, H.-U. (1989): The echolocation and hunting behavior of Daubenton's bat, *Myotis daubentoni.* Behav. Ecol. Sociobiol. **24**, 225–238.

Kulzer, E.; Bastian, H. V.; Fiedler, M. (1987): Fledermäuse in Baden-Württemberg. Beih. Veröff. Naturschutz Landschaftspflege Bad.-Württ. **50**, 1–152.

Müller, A. (1991): Die Wasserfledermaus in der Region Schaffhausen. Fledermaus-Anzeiger **28**, 1–3.

Müller, A.; Widmer, M. (1985): Zum Vorkommen der Langohrfledermäuse *Plecotus auritus* (Linnaeus, 1758) und *Plecotus austriacus* (Fischer, 1829) im Kanton Schaffhausen. Mitt. natf. Ges. Schaffhausen **32**, 215–222.

Nyholm, E. S. (1965): Zur Ökologie von *Myotis mystacinus* (Leisl.) und *M. daubentoni* (Leisl.) (Chiroptera). Ann. Zool. Fennici **2**, 77–123.

Pfister, H.-P. (1978): Die Schätzung von Feldhasenbeständen mit Hilfe der Scheinwerfer-Streifentaxation. Wildbiologie für die Praxis **3** (2), 1–9.

Rieger, I.; Walzthöny, D.; Alder, H. (1990): Wasserfledermäuse, *Myotis daubentoni,* benutzen Flugstraßen. Mitt. natf. Ges. Schaffhausen **35**, 37–68.

Schober, W.; Grimmberger, E. (1987): Die Fledermäuse Europas – kennen, bestimmen, schützen. Stuttgart: Franckh'sche Verlagshandlung.

Stutz, H. P. (1985): Fledermäuse im Kanton Schaffhausen. Neujahrblatt natf. Ges. Schaffhausen **37**, 1–40.

Wallis, W. A.; Roberts, H. V. (1960): Methoden der Statistik. Freiburg i. Br.: Rowohlt und Rudolf Haufe Verlag.

Anschrift der Verfasser: Dr. Ingo Rieger und Dr. Doris Walzthöny, Fledermaus-Gruppe Rheinfall, c/o BiKom Büro für integrale Kommunikation, Chratzhöfli 4, CH-8447 Dachsen, Schweiz

Z. Säugetierkunde 58 (1993) 13–17

ISSN 0044-3468

Zur Taxonomie der Amurkatze *(Felis bengalensis euptilura)*

Von A. Schreiber, W. Puschmann and H. Tichy

Zoologisches Institut der Universität Heidelberg, Deutschland, und Zoologischer Garten Magdeburg, Deutschland

Eingang des Ms. 31. 3. 1992
Annahme des Ms. 15. 7. 1992

Abstract

On the taxonomy of Amur cat (Felis bengalensis euptilura)

Nei's standard genetic distance between Amur cat (*Felis [bengalensis] euptilura*) and a tropical leopard cat (*Felis bengalensis* ssp.) amounted to 0.018, with glutamate-pyruvate-transaminase being the only observed differential marker among 29 electrophoretic loci. However, this enzyme is variable in wild cat (*Felis s. silvestris*), rendering its taxonomic use doubtful. Amur cat and tropical leopard cat both have a chromosomal complement of 38 chromosomes, including 34 (sub)metacentrics and four acrocentrics. Their standard genetic distance to pure-bred European wild cat measured 0.644.

Einleitung

Die Amurkatze aus dem sibirisch-mandschurischen Grenzgebiet gehört zur *Prionailurus*-Gruppe der Kleinkatzen und zeichnet sich vor ihren Nächstverwandten, den südlich anschließenden eigentlichen Bengalkatzen (*Felis bengalensis*), durch morphologische Eigenständigkeit aus (Elliot 1871; Dobroruka 1971; Heptner 1971; Heptner und Sludskij 1980). Seit ihrer Beschreibung als *Felis euptilura* (Elliot, 1871) wird ihre Systematik unterschiedlich interpretiert. In zahlreichen Faunenwerken als große nördliche Unterart der Bengalkatze (*Felis bengalensis euptilura*) angesehen, weisen Heptner (1971) und Heptner und Sludskij (1980) nach ausführlichen Vergleichen von Schädel- und Färbungsmerkmalen darauf hin, daß *Felis euptilura* als eigenständige Art eine phylogenetisch ursprüngliche Position einnehme, die zwischen Bengal- und Fischkatze (*Felis viverrina*) vermittle. Er stellt sie an den Ursprung seiner Formenreihe europäisch-nordasiatischer Kleinkatzen und vermutet die Kontaktzone zwischen *Felis euptilura* und *Felis bengalensis* im festländischen China. Auch Pocock (1939) gibt an, die Bengalkatzengruppe habe sich aus einem nördlichen Stammareal ausgebreitet. Die Amurkatze ist die größte Form der Bengalkatzengruppe. Die Gesamtlänge des Schädels adulter Kater beträgt 101,7–115,3 mm (Heptner und Sludskij 1980), gegenüber 89–102 mm bei indischen (Pocock 1939), und 80–90,5 mm bei javanischen Bengalkatzen (Sody 1949). Der Schwanz erreicht bei Amurkatzen nur ein Drittel der Körperlänge, gegenüber der halben Körperlänge bei benachbarten chinesischen Bengalkatzen (Dobroruka 1971).

Gelegentlich werden außergewöhnlich große Amurkatzen mit einer Körperlänge von 107 cm und einer Schwanzlänge von 44 cm beobachtet (durchschnittliche Körperlänge von Männchen: 60–85 cm). Manche Felle erreichen Luchsgröße. Solche Riesenformen werden als Mischlinge mit streunenden Hauskatzen gedeutet, mit welcher uneingeschränkte Kreuzbarkeit angegeben wird (Heptner und Sludskij 1980). Stroganov (1969) hebt den phänotypischen Polymorphismus der Art hervor, aufgrund dessen man zunächst fälschlich zwei Spezies im Amurgebiet unterschied. Rund 20 synonyme taxonomische Artnamen zur Bengalkatze deuten deren Formenvielfalt an (Stroganov 1969). Dobroruka (1971) beschrieb eine Serie von 320 koreanischen Amurkatzenfellen und beobachtete Musterunterschiede zu chinesischen Bengalkatzen sowie individuelle Färbungsvarianten.

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5801-0013 $ 02.50/0

Die Bereitstellung von Blutproben durch den Zoologischen Garten Magdeburg ermöglichte einige genetische Vergleiche der Amurkatze mit der tropischen Bengalkatze sowie mit Waldwildkatzen.

Material und Methoden

Beide untersuchte Amurkater stammen von Wildfängen aus dem Amurgebiet ab, die über Rostov/Don (Rußland) nach Magdeburg importiert worden waren. Ein Kater der Bengalkatze ist tropischer Herkunft, aber subspezifisch nicht eindeutig zu bestimmen. Die beiden männlichen Waldwildkatzen (*Felis s. silvestris*) entstammen der Population des Unterharzes. Zu Vergleichszwecken wurden vom Howlett Zoo (Bekesbourne, England) Serumproben vom Schneeleoparden (*Panthera uncia*), Geparden (*Acinonyx jubatus*) und von der Steppenkatze (*Felis silvestris ornata*) zur Verfügung gestellt. Chromosomendarstellung und elektrophoretische Techniken wurden andernorts geschildert (Schreiber 1991; Schreiber et al. 1992). Die Tabelle stellt die untersuchten Proteine sowie die verwendeten Elektrophoresepuffer zusammen. Liegen zwei Isoenzyme in einem System vor, werden diese vom anodischen Pol ausgehend numeriert. Molekulargewichtsbestimmungen denaturierter Serumpeptide erfolgten mit SDS-Polyacrylamid-Elektrophorese.

Ergebnisse

Die Karyotypen der männlichen Amurkatze und eines tropischen Bengalkaters sind nach Giemsa-Färbung nicht zu unterscheiden. Sie umfassen jeweils 38 Chromosomen (NF = 74), darunter 34 (sub)metazentrische und zwei akrozentrische Autosomen und stimmen mit den Chromomenbildern zweier früher untersuchter Bengalkatzen unbekannter Herkunft überein (Wurster-Hill und Gray 1973). Das Y-Chromosom ist das kleinste Chromosom. Das Komplement der Haus- und Waldwildkatze (38 Chromosomen, NF = 72) unterscheidet sich bei ansonsten weitgehender Ähnlichkeit dadurch, daß zwei akrozentrische Autosomenpaare vorliegen.

Von 29 untersuchten Proteinen war nur ein elektrophoretisch charakterisierter Allozym-Locus, die Glutamat-Pryuvat-Transaminase (*GPT*), zwischen Amurkatze (*GPT bb*) und tropischer Bengalkatze (*GPT aa*) verschieden, indem letztere ein weiter anodenwärts bandendes Zymogramm aufwies. Damit ergibt sich formal eine Neische Standard-Distanz (Hillis und Moritz 1991) von 0,018. Jedoch war *GPT* bei den beiden Waldwildkatzen variabel, indem ein Tier das anodische Muster wie bei der Bengalkatze (vermutlich homozygot *GPT aa*) aufwies, während das andere heterozygot für beide Allele war (*GPT ab*). Wenn auch *Prionailurus GPT*-Varianten aufweist, ist es möglich, daß die angegebene Allozym-Distanz durch ungleiche Fixierung eines Polymorphismus in den minimalen Stichproben zustande kam. Die Nei-Distanz für kleine Stichproben (Hillis und Moritz 1991) muß denn auch auf 0,00 korrigiert werden. Im Vergleich zu dieser sehr geringen Distanz ist die Waldwildkatze von beiden *Prionailurus*-Formen deutlich differenziert: die Standard-Distanz beträgt 0,644. Nur acht Proteine ließen sich nicht elektrophoretisch unterscheiden: *ACP, MDH, AK, 6-PGD, Gd, ICD, GLUDH* und *Albumin*. Bei *Hbα* und *HBβ, ADA, CA-2, SOD, ES* (gefärbt mit α-Naphthylacetat), *LDH-A, NP, GLO, PGM-1, E* (Plasma), Postalbumin-1, Postalbumin-2 und Transferrin wanderten die Allele von *Prionailurus* weiter anodenwärts, während bei *CA-1, ES* (gefärbt mit 4-Methyl-umbelliferylacetat), *LDH-B, GPI, PGM-2* und α-1-Antitrypsin die Bandenmuster der Waldwildkatze erhöhte anodische Mobilität aufwiesen.

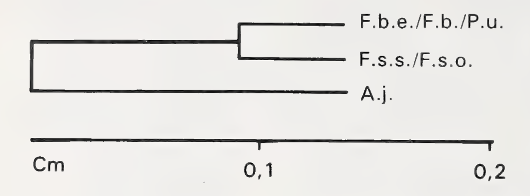
Die Molekulargewichte von 22 Serumproteinen zwischen 15 000 Da und 116 000 Da stimmten bei Amur- und tropischer Bengalkatze ausnahmslos überein, ebenso zwischen Waldwildkatze und Hauskatze. Der Besitz zweier Peptide von 38 500 Da und 100 000 Da unterschied beide *Prionailurus*-Formen von der Waldwildkatze, wo sie durch Proteine anderer Molekülmasse ersetzt waren (wobei die genaue Homologie offen bleibt). Zur Einordnung dieser Beobachtung wurden die Molekulargewichte der Serumproteine mit

Elektrophoresebedingungen

Wenn nicht anders vermerkt, wurde verdünnter Brückenpuffer als Gelpuffer verwendet. Die Trennungen erfolgten in 1 mm dünnen Agarosegelen oder durch isoelektrische Fokussierung (IEF) in 300 μm dünnen Polyacrylamidgelen

Protein	Locuszahl	Elektrophoresepuffer
	Erythrocytenproteine	
Lactat-Dehydrogenase *(LDH)*	2	200 mM Natriumphosphat pH 7,0
Malat-Dehydrogenase *(MDH)*	1	40 mM Citrat ph 6,1
6-Phosphogluconat-Dehydrogenase *(PGD)*	1	100 mM Natriumphosphat pH 7,0
Glucose-6-phosphat-Dehydrogenase *(Gd)*	1	100 mM Natriumphosphat pH 7,0
Adenylatkinase *(AK)*	1	410 mM Citrat pH 7,0 (Gel: 5 mM His-HCl pH 7,0)
Adenosindesaminase *(ADA)*	1	100 mM Na-Phosphat pH 6,5
Isocitrat-Dehydrogenase *(ICD)*	1	250 mM NaH_2PO_4/150 mM Citrat pH 5,9
Nucleosidphosphorylase *(NP)*	1	40 mM LiOH/440 mM Borat pH 7,2
Phosphoglucomutase *(PGM)*	2	IEF Servalyt pH 5–7
Glutamat-Pyruvat-Transaminase *(GPT)*	1	200 mM Tris/200 mM Maleat/100 mM EDTA/ 200 mM $MgCl_2$/225 mM NaOH pH 7,2
Saure Phosphatase *(ACP)*	1	20 mM NaH_2PO_4/15 mM Na-Citrat/1 mM EDTA pH 5,8
Superoxid-Dismutase *(SOD)*	1	IEF Servalyt pH 5–7
Carboanhydrase *(CA)*	2	65 mM Tris/35 mM Borat / 2 mM EDTA pH 8,6
Erythrocytenesterasen *(ES)*	2	100 mM Tris/100 mM Maleat pH 7,2
Glyoxalase *(GLO)*	1	200 mM Tris/His-HCl pH 7,8
Glucosephosphat-Isomerase *(GPI)*	1	60 mM LiOH/300 mM Borat pH 8,1 (Gel: 30 mM Tris/5 mM Citrat pH 8,5)
Hämoglobin *(Hb)*	2	IEF Servalyt pH 7–8
	Plasmaproteine	
Pseudocholinesterase *(E)*	1	300 mM Borat pH 8,0 (Gel: 76 mM Tris/ 7 mM Citrat pH 8,6)
Glutamat-Dehydrogenase *(GLUDH)*	1	135 mM Tris/Citrat pH 7,0
Transferrin	1	IEF Servalyt pH 4–6
Postalbumine	2	Tris/Borat pH 8,6
Albumin	1	IEF Servalyt pH 4–6
α-1-Antitrypsin	1	IEF Servalyt pH 4–6

denen weiterer Feliden verglichen und die Musterähnlichkeit in einem UPGMA-Phänogramm dargestellt (Abb. 1). Die 100-kDa- und 38,5-kDa-Marker, deren Besitz die Seren von *Prionailurus* von jenen der Waldwildkatze/Hauskatze unterscheiden, fanden sich in identischer Weise beim Schneeleoparden, nur das 100-kDa-Peptid ebenfalls beim Geparden, welcher auch im hochmolekularen Bereich das abweichendste Peptidmuster aufwies. Die Molekulargewichte der Serumproteine stimmten zwischen Waldwildkatze und der nahe verwandten Steppenkatze ausnahmslos überein, aber auch zwischen *Prionailurus* und dem Schneeleoparden. Das zeigt, daß die genetische Differenzierung auch von unbestrittenen Katzenspecies nicht ausgeprägt genug ist, um die Molekulargewichte ihrer Plasmaproteine wesentlich zu berühren.



UPGMA-Phänogramm der Molekulargewichtsdivergenz von 22 Serumproteinen (15 000–116 000 Da), ermittelt mit SDS-Polyacrylamid-Elektrophorese in 10 %igen Laemmli-Gelen. Die relativen Distanzen beruhen auf Czekanowski-Distanzen (Cm) des gemeinsamen Besitzes bzw. der übereinstimmenden Abwesenheit von Peptiden identischer Molekülmasse. Das Schaubild beruht auf sehr wenigen differenzierenden Merkmalen (siehe Text). *F.b.e./F.b./P.u.* = Amur/Bengalkatze/Schneeleopard, *F.s.s./F.s.o.* Waldwild-/Steppenkatze, *A.c.* = Gepard

Die nativen Elektrophoresemuster ließen bei den einbezogenen drei Individuen von *Prionailurus* in keinem Fall auf biochemischen Polymorphismus schließen, dagegen zeigten bei der Waldwildkatze vom Unterharz *GPT, PGM-2,* Transferrin und vielleicht eine Erythrocytenesterase (α-Naphthylacetat) je zwei Varianten, welche als heterozygote Muster interpretiert werden können.

Diskussion

Aufgrund der phylogenetischen Konservierung der Chromosomenbilder bei Feliden (Wurster-Hill und Centerwall 1982) ist die Übereinstimmung der Karyotypen von Amur- und Bengalkatze kein ausschlaggebendes Argument für deren artlichen oder unterartlichen Status. Das Taxonpaar Amurkatze/Bengalkatze stellt ein Beispiel für recht deutliche morphologische Differenzierung bei geringer genetischer Divergenz dar. Letztere ist so schwach ausgeprägt, daß sie nur mit erheblich größeren Stichproben als gegenwärtig in Europa verfügbar mit letzter Sicherheit quantifiziert werden kann. Bei zahlreichen Säugetieren würde eine Standard-Distanz von 0,018 noch nicht einmal unterartliche Sonderung anzeigen. Daher halten wir es für unwahrscheinlich, daß die Amurkatze eine eigenständige Art darstellt. P. Leyhausen (in litt. 1992) kommt nach dem Vergleich von Schädeln zum gleichen Befund. Allerdings bleibt eine endgültige taxonomische Wertung Arbeiten zum Verhalten der *Prionailurus*-Formen vorbehalten, um zu erkennen, ob im noch näher zu beschreibenden chinesischen Kontaktgebiet die Fortpflanzung zwischen beiden Formen trotz geringer genetischer Differenzierung eingeschränkt ist, z. B. durch Unterschiede in der Lebensweise. Das Vorkommen von Hybriden mit verwilderten Hauskatzen (Heptner und Sludskij 1980) schwächt diesen Einwand ab. Die morphologische Affinität, die Heptner und Sludskij (1980) zwischen Amurkatze und *Felis silvestris* erkennen, beruht auf Konvergenz oder gemeinsamer Retention ursprünglicher Merkmale, keinesfalls aber darauf, daß die Amurkatze eine verwandtschaftlich zwischen Bengalkatze und Waldwildkatze vermittelnde Position einnimmt.

Innerartliche Größenunterschiede und synökologische oder bioklimatische Regelmäßigkeiten in der Formenmannigfaltigkeit von Landraubtieren haben das Interesse zahlrei-

cher Zoologen gefunden (Gittleman 1985), aber nur bei sehr wenigen Beispielen für die Bergmannsche oder Allensche Klimaregeln kann man die Abwandlung des äußeren Erscheinungsbildes mit Daten zur biochemischen Differenzierung korrelieren. Bei Tigern (*Panthera tigris*) liegen Daten in einem vergleichbaren Fall vor: Goebel und Whitmore (1987) ermittelten elektrophoretisch eine Standard-Distanz von 0,0098 zwischen zoolebenden Amur- und tropischen Tigern. O'Brian et al. (1987) beschreiben Neis Standard-Distanzen zwischen zoolebenden Amurtigern und Sumatratigern mit 0,003, und zwischen Amur- und Bengaltigern mit 0,007. Beide Distanzwerte schrumpfen auf 0,00, wenn die geringen Stichprobengrößen Berücksichtigung finden.

Zusammenfassung

Das Chromosomenkomplement der Amurkatze besteht aus 38 Chromosomen (NF = 74) und stimmt mit dem der tropischen Bengalkatze überein. Die elektrophoretische Standard-Distanz (nach Nei) zwischen der morphologisch recht verschiedenen Amur- und tropischen Bengalkatze auf der Basis von 29 Proteinloci beträgt 0,018, erweist sich aber nach Berücksichtigung von Stichproben-Effekten als nicht signifikant. Der einzige Allozymunterschied betrifft die Glutamat-Pyruvat-Transaminase, die bei der Waldwildkatze polymorph war. Die Standard-Distanz der beiden *Prionailurus*-Formen zur Waldwildkatze fällt mit 0,644 relativ deutlich aus.

Literatur

Dobroruka, L. J. (1971): Individual variation of the Amur leopard cat, *Prionailurus bengalensis euptilurus* (Elliot, 1871) from Korea. Vestn. Cesk. Spolecnoi Zool. **35**, 9–10.

Elliot, D. G. (1871): Remarks on various species of Felidae, with a description of a species from North-Western Siberia. Proc. Zool. Soc. (Lond.), 758–761.

Gittleman, J. L. (1985): Carnivore body size: ecological and taxonomic correlates. Oecologia (Berlin) , 540–554.

Goebel, A. M.; Whitmore, D. H. (1987): Use of electrophoretic data in the reevaluation of tiger systematics. In: Tigers of the world. Ed. by R. L. Tilson, U. S. Seal. Park Ridge (New Jersey): Noyes Publications. S. 10–27.

Heptner, V. G. (1971): [Über die systematische Stellung der Amurwildkatze und einiger anderer ostasiatischer Katzen, die *Felis bengalensis* Kerr, 1792 zugeordnet werden.] Zool. Zurn. **50**, 1720–1727 (russ., engl. Zus.).

Heptner, V. G.; Sludskij, A. A. (1980): Die Säugetiere der Sowjetunion. Band III: Raubtiere (Feloidea). Jena: Gustav Fischer.

Hillis, D. M.; Moritz, C. (1990): Molecular systematics. Sunderland (Mass.): Sinauer Ass.

O'Brien, S. J.; Collier, G.; Benveniste, R.; Nash, W.; Newman, A.; Simonson, J.; Eichelberger, M.; Seal, U.; Janssen, D.; Bush, M.; Wildt, D. (1987): Setting the molecular clock in Felidae: The great cats, *Panthera*. In: Tigers of the world. Ed. by R. L. Tilson, U. S. Seal. Park Ridge (New Jersey): Noyes Publications. S. 10–27.

Pocock, R. I. (1939): The fauna of British India, including Ceylon and Burma. Mammalia, Vol. 1. London: Taylor and Francis.

Schreiber, A. (1991): Molekulare Individualität und Naturschutz. Populationsgenetische Beiträge zur Erhaltung bedrohter Arten. Diss., Univ. Heidelberg.

Schreiber, A.; Nötzold, G.; Held, M. (1993): Molecular and chromosomal evolution in anoas (Bovidae: *Bubalus* spec.). Z. zool. Syst. Evolut.-forsch. **31** (im Druck).

Sody, H. J. V. (1949): Notes on some Primates, Carnivora, and the babirusa from the Indo-Malayan and Indo-Australian regions, with descriptions of 10 new species and subspecies. Treubia **20**, 121–190.

Stroganov, S. U. (1969): Carnivorous mammals of Siberia. Jerusalem: Israel Prog. Scient. Trans.

Wurster-Hill, D. H.; Centerwall, W. R. (1982): The interrelationships of chromosome banding patterns in canids, mustelids, hyena, and felids. Cytogenet. Cell Genet. **34**, 178–192.

Wurster-Hill, D. H.; Gray, C. W. (1973): Giemsa banding patterns in the chromosomes of twelve species of cats (Felidae). Cytogenet. Cell. Genet. **12**, 377–397.

Anschriften der Verfasser: Dr. Arnd Schreiber, Zoologisches Institut der Universität, Im Neuenheimer Feld 230, W-6900 Heidelberg; Dipl.-Biol. Wolfgang Puschmann, Zoologischer Garten Magdeburg, Am Vogelgesang, O-3017 Magdeburg; Dr. Herbert Tichy, Max-Planck-Institut für Biologie, Spemannstraße 34, W-7400 Tübingen, Deutschland

Z. Säugetierkunde 58 (1993) 18–30

ISSN 0044-3468

Agonistic behaviour in captive Babirusa *(Babyrousa babyrussa)*

By A. A. Macdonald, D. Bowles, Justine Bell, and Kristin Leus

Department of Preclinical Veterinary Sciences and the School of Agriculture, University of Edinburgh, Edinburgh, Scotland, and Jersey Wildlife Preservation Trust, Trinity, Jersey, Channel Islands

Receipt of Ms. 24. 2. 1992
Acceptance of Ms. 13. 7. 1992

Abstract

The agonistic behaviour of captive babirusa *(Babyrousa babyrussa celebensis)* was studied at zoos in Indonesia, Belgium, and the Channel Islands. Observations were carried out on ninety-five babirusa of which 25 males and 21 females were kept in Surabaya Zoo, Indonesia. Male-male, male-female and female-female interactions were analysed with respect to body size, shape of upper canines, age and sex. The agonistic behaviour was described and could be categorised. "Threat at a distance", "surprise rush", and "the lying lunge" were used frequently by both males and females. The submissive babirusa generally lowered its head and vocalised its submission by means of a repeated, breath-long, rumbling squawk. The canine teeth were never seen to be used as weapons. "Boxing" was the ultimate form of agonistic behaviour exhibited between male babirusa. Body size was the most important factor determining the outcome of a "boxing" match. "Boxing" between females was never observed. Female agonistic behaviour was mainly aimed at biting the forelimb of the opponent. Adult females were submissive to adult males, but adult females were dominant over sub-adult males. Large females were dominant over smaller females.

Introduction

The babirusa is endemic to the Indonesian islands of Sulawesi, Buru and the smaller Sula and Togian islands. Very few observations have been made of babirusa in the wild. One study of the behaviour of five animals was performed on the Togian island of Pangempan (Selmier 1983) and recently video recordings of wild babirusa were made on the northern mainland of Sulawesi (Patry and Capiod 1989; Patry 1990). Several other behavioural studies have been made on captive animals. These either describe the social behaviour of very small numbers of captive animals, are preliminary accounts of observations on larger groups or are detailed accounts of reproductive behaviour (Geoffroy-St-Hillaire and Cuvier 1842; Selmier 1978, 1983; Bowles 1986; Macdonald et al. 1989; Leus et al. 1992).

The few studies of the babirusa in the wild and in captivity suggest that they are social animals, one or more adult females living together with young and juveniles, the adult males solitary or singly associated with family groups. They appear to employ a range of behaviours, to obtain or maintain dominance and position. This study reports on a variety of agonistic behaviour found between individual babirusa.

Material and methods

Observations were made largely at Surabaya Zoo, Indonesia with additional observations recorded on the Channel Islands at the Jersey Wildlife Preservation Trust, at the Royal Zoological Society of Antwerp, Belgium, and in Ragunan Zoo, Jakarta, Indonesia. In July and August 1987 and 1988 between 0500 h (one hour before sunrise) and 2200 h (four hours after sunset) observations were carried out on 25 male and 21 female babirusa in six adjacent and inter-connecting pens in Surabaya Zoo. The main enclosure housed up to 35 animals, and details of the layout and sizes of the pens were published earlier (Macdonald et al. 1989). Vocalisations were recorded on tape and subsequently analysed and described in relation to the behaviour with which they were associated.

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5801-0018 $ 02.50/0

The results of 220 of the agonistic encounters observed in 1988 at Surabaya Zoo were grouped in the following way. A sample of 142 observations of the outcome of fighting behaviour (boxing) between male babirusa was analysed. Precise ages were unknown, but the males were classified into four subgroups, according to the following criteria:

juvenile: (small sized body, upper canines are just appearing)
sub-adult: (body smaller than the adult male, canines narrow and upper canines tightly curved)
adult: (large body size, canines thick, the upper canines curved back towards the head or are broken and more straight, dewlap present)
old adult: (large body size, skin is scarred, creased and folded, upper canines usually broken and more vertical).

A further sample of 32 observations listed the results of agonistic male-female behaviour which were analysed according to sex and 'age' subgroups. A third sample of 50 observations examined the outcome of confrontations between female babirusa which were classified into three subgroups; juveniles, small adults and large adults.

In 1991, Surabaya Zoo moved its remaining 13 males and 16 females to a single new pen 35 m × 15 m in area. The animals were observed in December 1991 and January 1992 between 0500 h and 1500 h. Particular attention was paid to the agonistic behaviour in its different component parts shown by the dominant male of the group. In additon, the agonistic behaviour shown by the females towards one another and to the males was examined. Additional observations, which were gathered from a further forty-nine babirusa are included in this report; these were collected during studies of behaviour at the Jersey Wildlife Preservation Trust from 1983–1987, at Ragunan Zoo, Indonesia during the months of July and August 1987 and at the Royal Zoological Society of Antwerp, Belgium from July 1989–91.

Results

The agonistic behaviour could be allocated to seven different categories by using the terms "threat at a distance", "surprise rush", "nose in the air", "head under jaw submission", "front half supported", "boxing", and "the lying lunge".

Male-male interactions

"Threat at a distance"

The dominant male needed only look, or make an upward thrust or toss of the head in order to threaten another male. The threatened animal moved cautiously in relation to the dominant male though not necessarily far from him and seemed to keep a close eye on his movements. When a threat was perceived the submissive animal lowered his head and uttered a breath-long rumbling squawk, which may be repeated.

"Surprise rush"

Males often made sudden, and apparently unprovoked charges at other males. This startled the attacked male into facing the onrushing animal, lowering his head and uttering the rumbling squawk sound of submission. Usually these attacks were not carried through to physical contact; the attacking male charged forward with his head held high for a short distance only. However, in those few instances when the charge was carried through, the mandibular canine of the attacker struck the upper and/or lower canines or the shoulder of the submissive animal. If the attacked male was not intimidated the attacker became the attacked. The dominant male ended a standing confrontation by walking away.

"Nose in the air"

Two or more animals approached each other with their heads raised and their noses held in the air. They manoeuvred with their heads held high and at 60 to 240 degrees to one another (Fig. 1). The animals backed off slowly and then suddenly rushed several steps forward, again with heads raised and noses elevated. This complex of circling and feinting manoeuvres could either develop further, or the animals wandered away from each other.

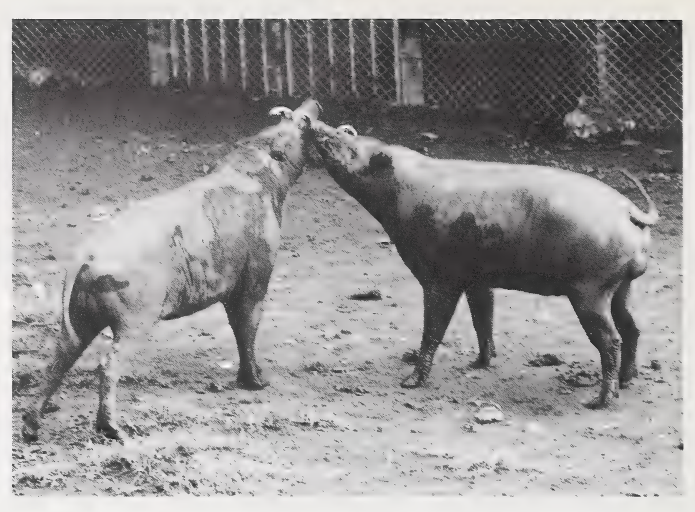


Fig. 1. Two adult male babirusa demonstrating the "nose in the air" agonistic behaviour

"Head under jaw submission"

When two males were in close proximity the submissive animal took up a position at an angle, often at about 90 degrees, to the head of the dominant animal, lowered its head such that its nose was positioned under the mandible of the superior male and uttered a very short squawk or a continuous rattling stream of sound, the pitch and intensity of which increased as the animal seemed to perceive increased threat. The dominant male made a sucking "tuh" sound apparently by lowering its mandible and then pulling its tongue off the upper palate. Both males circled one another with the subordinate animal usually in the middle. Even after being nipped in the nose or mouth, the subordinate male did not give up but remained where he was, often complaining noisily. In some instances the dominant male turned rapidly to face another male in close proximity and the behaviour was repeated. Usually the dominant male seemed to be the one to break off the confrontation by ignoring his opponent and wandering off.

"Front half supported"

Two males approached one another such that their heads were held side by side and pointing in the same direction. Their bodies were often held at 60 degrees to one another. The animals manoeuvred side by side until one male mouthed the tusks of the other and layed his head on the snout of the other. If this manoeuvre was successful, the male whose head was highest leant his head on the head of the other male (Fig. 2). The two animals could be at an angle or facing one another. Often the upper male seemed to be actively pushed upwards by the lower animal until his forefeet were off the ground. Sometimes he actively climbed until his chest was on the head of the inferior animal (Fig. 3). The upper male paddled with his front legs against the back and shoulders of the lower animal. The position of the canine teeth of the lower animal was such that they rubbed on the exposed neck and chin of the upper animal (Fig. 2), but without causing damage. This position was maintained for a variable length of time, the lower animal sometimes uttering the submissive squawk. It was the superior male which ended the behaviour by dismounting and walking away from the other male.

On one occasion, when two relatively young (2–3 years) males were squabbling in a narrow corridor, the hind legs of the upper male slipped and he lost the grip of his forefeet



Fig. 2. Two adult male babirusa engaging in an early stage of the "front half supported" behaviour. Note that the maxillary canines of the lower male are in contact with the neck of the superior animal

on the back and shoulders of the lower male. The two animals had manoeuvered into a 90 degree angle with each other and as the superior animal lost his balance the inferior animal tossed his head. The left lower canine of the lower male struck the neck of the falling male and penetrated about 3 cm. The upper male became locked on the tusk of the lower male and started a loud, continuous, high pitched scream. The lower male persisted in making upward movements with his head. He made no attempt to end the confrontation. The animals were eventually separated by the keepers. The animal with the pierced neck behaved in a very submissive fashion for weeks thereafter.

"Boxing"

Only about 5 % of interactions resulted in boxing behaviour. Boxing usually started from the "nose in the air" behaviour with both animals facing each other and each trying to place his head on top of that of the other animal. Each raised himself off the ground until both were standing on their hind legs facing one another. Once in this position they leant and paddled against the chest and shoulders of their opponent (Fig. 4). Their snouts were held as high as possible. The animals seemed able to remain on their hind legs for about one minute at a time. If one of the animals fell onto all four legs it reared up again and the boxing continued. The boxing match usually lasted for 2 to 5 minutes, but could extend for up to 20 minutes. The pushing and shoving could lead to large distances being covered within the pen. During the boxing the animals often fought with their mouths open but there was little or no vocalisation.

The superior animal often appeared to be the one that raised his head the highest; he also had his ears pointed forward. The dominant male usually broke off the confrontation by ignoring his opponent and wandering off. The submissive animal may or may not lower his head below that of the doimant animal when they both came back onto all fours but rarely did he vocalise his submission with the short squawk or continuous rattling stream



Fig. 3. The final stage of "front half supported" behaviour as exhibited by two male babirusa. The neck and chest of the upper male rest on the face and teeth of the lower male

of sound described above. Occasionally a third male intervened by raising his head between the competing animals and causing the boxing match to stop. In some instances, the intruder himself began boxing with one of the two combatants. It also happened that the intruding male would join forces with one of the two combatants and the third animal would then back off in the face of the two advancing males.

The deciding factor seemed to be the ability to stretch the highest and push your opponent off balance and onto all four legs. The tusks seemed to play little or no part in the contest (Fig. 4). The contests could become violent in which case the males made greater use of their strength and threw their weight at one another. In those instances the upper male uttered a rolling, deep-throated, low pitched growl and would often froth at the



Fig. 4. "Boxing" behaviour being demonstrated by two adult male babirusa. Both animals have reared onto their hind legs, faced one another, and are leaning and paddling with their forefeet against the chest and shoulders of their opponent. Note that their noses are being stretched as high as possible

mouth. These battles attracted the attention of other males which often interfered in the fight and broke it up.

An analysis of 72 boxing encounters between males of different size showed that the larger male was dominant on 71 occasions. In 28 further encounters where the males were evenly matched for size, straight tusked animals were dominant 16 times and those with curved tusks were dominant 12 times. When age of the animal was examined during another 38 encounters, sub-adult or adult males were dominant over elderly males on 30 occasions. No clear outcome was apparent in the remaining eight interactions, and in four other boxing matches no distinguishing feature was apparent between the animals.

Boxing was most common among the young adult males. Old males were never seen boxing and often seemed to ignore conflict except for vocalisation and biting at animals when food was available. In the winter of 1991/92 the alpha male, which was not the largest male in the group, was rarely seen boxing. However, he patrolled the pen almost constantly and showed the other types of intimidatory behaviour on many occasions. Infants of only a few days of age were seen pushing each other and attempting to get on top of each other. Siblings of either sex and aged from about two months until weaning were seen to rear up on their hind legs and playfully paddle against one another's chests with their forelegs. More serious boxing between males was observed when the juveniles were about one year of age, when the tusks were emerging. Boxing could take place at any time of the day but usually did so more often when it was cooler, in the early morning and late in the afternoon.

"The lying lunge"

When lying in the pen a male was sometimes seen to swing his head up and round towards an approaching animal which appeared to be about to lie down beside him. A loud shriek of short duration (< 1 sec) was usually uttered by the submissive pig. The threat was sometimes followed by a nip at the nose, flank or leg of the threatened animal.

Male-female interactions

Intimidatory behaviour of the three types, "threat at a distance", "surprise rush" and "the lying lunge" were found between males and females in which either sex may be dominant. The "head under jaw submission" with squealing vocalisation was seen in association with both reproductive behaviour and perceived threat. The female tended to bite at the front legs during an attack and would do so also in defence. When the female nipped defensively at the feet of the male he uttered a low "gruff-gruff" sound. Only twice was an adult female seen to come to an adult male with her nose raised in the same way as was described between two adult males; when this happened they manoeuvered to face each other, and began boxing. Neither animal vocalised.

On one occasion the same female repeatedly climbed onto the front of the same male until her chest rested on his head. He terminated the interaction by moving away without a sound.

In 31 of 32 interactions between adult males and females, the male was dominant. When an adult female confronted either a sub-adult or juvenile male the adult female dominated in 11 out of 13 occasions. In five interactions between juvenile animals the males were dominant.

Female-female interactions

Examples of "distant threat", "surprise rush" and "the lying lunge" have been seen between females. Usually, when one female rushed at another, the attacked female ran off closely pursued for some distance by the attacking female. We often saw the dominant female chase the submissive female repeatedly over a period of about ten minutes.



Fig. 5. Typical agonistic behaviour between two adult females in which the female on the right is attempting to reach below the head and neck of the female on the left in order to bite the latter's front leg. The female on the left has anticipated this move and has lifted her right front foot away to prevent it from being bitten

Of the other four behaviours, "nose in the air" and "head under jaw submission" were seen rarely between adult females and "front half supported" and "boxing" behaviours were never seen. When two females confronted one another it was often quite violent, fast moving and noisy. Clear attempts were made to reach below the head and neck of one another; the objective seemed to be to bite the leg or foot of the opponent (Fig. 5). The female which had her head highest and allowed her fore or hind limb to be bitten lost the contest and uttered a high pitched squeal of short duration. The superior female often expressed a deep-throated growl during the contest. Fifty female-female interactions were observed and in 41 of these the larger animal was dominant. In only four occasions was the smaller female superior. On five occasions the interacting females were of the same size.

When single females were put in adjacent wire-sided enclosures two different reactions were observed. Some females appeared indifferent of one another whereas others would repeatedly show aggression towards each other. The latter would run back and forth along the separating fence with their heads elevated and ears pointed forward, making sharp upward thrusts of the head towards their opponent. They also often pushed side to side through the fence and growled at one another, nipping with their lower incisors in the direction of the legs and flanks of their opponent.

Discussion

We have identified and described a series of agonistic behaviours of the babirusa. These results confirmed and extended the fragmentary observations reported for this species by Selmier (1978, 1983), Macdonald et al. (1989), and Leus et al. (1992). The repertoire of behaviours exhibited by the babirusa fell within the broad classifications of threatening, display and fighting behaviour which are used for assessment between individuals of a wide variety of species (Maynard Smith 1982). The babirusa seems to employ the behaviours "threat at a distance", "nose in the air" and "boxing" as the sequence of increasing level of threat.

The same classifications can be recognised in the range of agonistic behaviours described for a number of pig species including the wild boar *(Sus scrofa),* the bush pig *(Potamochoerus porcus),* the warthog *(Phacochoerus aethiopicus)* and the giant forest hog *(Hylochoerus meinertzhageni)* although it is clear from the published descriptions that the details of the behaviours exhibited vary between genera (Frädrich 1965, 1967; Beuerle 1975; Cumming 1975; Skinner et al. 1976; Kingdon 1989).

"Threat at a distance" as demonstrated by the babirusa with a slow or faint movement of the head upwards has also been reported for the wild boar, the warthog and the bushpig (Frädrich 1965, 1967; Cumming 1975; Seidack 1990). A more overt toss of the head into the air in the direction of the opponent is shown by all pigs (Frädrich 1967).

Display is reported in the wild boar as the presentation of the body broadside to the opponent with the back arched, the front part of the body stretched out, the head elevated and the hair of the body erect (Frädrich 1967; Beuerle 1975). By way of contrast, bush pig opponents face one another, thereby presenting to one another their conspicuously marked head and erected dorsal main (Skinner et al. 1976; Seydack 1990). The only behaviour exhibited by the babirusa which could be identified as the equivalent of display was stretching of the head and "nose in the air". The animals will sometimes do this at a distance, but more usually close to their opponent and, like the warthog, may exhibit a range of positions from parallel head to head to frontal nose to nose (Frädrich 1965; Cumming 1975).

The subspecies of babirusa from Sulawesi, unlike the other two subspecies of babirusa, lacks the hair coat of the wild boar. The species also lacks the conspicuous facial colouration of the bush pig and the facial warts of the warthog. However, the male babirusa has prominent maxillary canines which grow upwards in such a way that they pierce through the skin of the snout and curve over in front of the forehead (Figs. 1–4 and 7). The lower canines grow upwards alongside the snout and curve more gradually caudally. Whether the canines are important to display is not known. Moreover, whether those babirusa subspecies with longer hair coats use these in display also remains a matter for speculation.

"Boxing" was the ultimate form of agonistic behaviour exhibited by the babirusa under observation in the zoos. This form of agonistic behaviour has not been reported for any other species of pig with the exception of *Sus scrofa cristatus,* on the island of Sri Lanka (Barrette 1986). One of the main differences between these two sets of observations

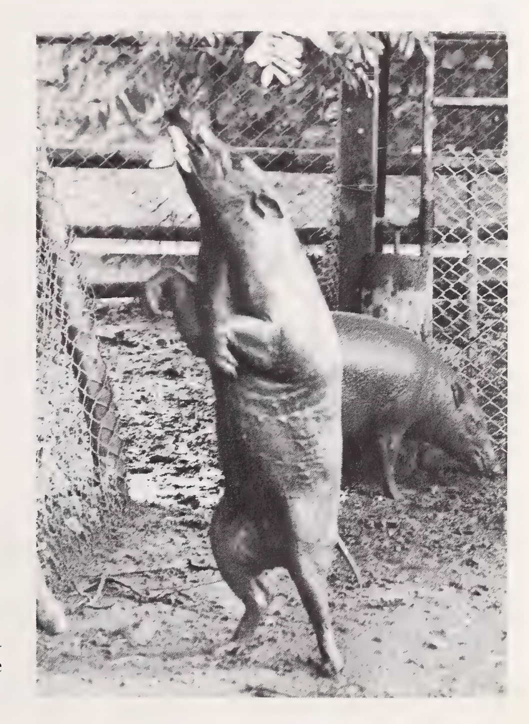


Fig. 6. An adult female balancing on her hind legs while browsing the leaves of a tree in the enclosure

concerns the female animal; adult female babirusa were never seen to box with one another whereas this did occur between female wild boar. Female babirusa did have the ability to balance on their hind limbs, and were seen browsing in this position (Fig. 6). They were also occasionally seen to box with male babirusa whereas adult male and female wild boar were never observed boxing with one another (Barrette 1986). Another difference was that the babirusa would repeatedly rear up on their legs if they slipped or were toppled momentarily, whereas the first occasion that the wild boar was knocked off balance decided the competition (Barrette 1986). The third main difference between the two species was the lack of retreat shown by the babirusa when defeated; the superior animal, which was usually the largest and the one which stretched the tallest on its hind limbs, walked away from the loser. This is in marked contrast to the pursuit of the loser shown by the wild boar (Frädrich 1967; Beuerle 1975; Barrette 1986).

It is possible that "boxing" may not represent the most extreme form of fighting behaviour in babirusa. Barrette (1986) suggested that the behaviour shown by the wild boar in Sri Lanka was a mechanism allowing delay or avoidance of the relatively high risks inherent in a tusk fight between wild boar, as has been described for this species by Beuerle (1975). Male babirusa have large canine teeth (Fig. 7) which are either absent or rudimentary in the female (Mohr 1960). It has been suggested that the upper canines may be used by one animal to hook one of the lower canines of his opponent; in this way the sharp maxillary canine of the opponent would be disarmed while he was free to inflict injury with his own lower canine to the opponent's eye, the side of his face or throat (Geist 1966; MacKinnon 1981).

Our study of the anatomy of the maxillary canine showed that conflict of this sort is unlikely. The maxillary canine has a relatively shallow socket, whereas that of the lower canine occupies a large proportion of the length of the mandible (Fig. 7). This implied that large leverage forces would be placed on the root of the upper canine by the well anchored lower canine of the opponent during this suggested hooking manoeuvre (MacKinnon 1981; Whitten et al. 1987) which the socket of the upper tooth would not be competent to withstand. Moreover, the upper canine has been described as loose in its socket (Mohr 1960) and not very strong, being liable to split or break (Heinsius and Vogt 1916; Mohr 1960; Schaftenaar 1991). On no occasion did we observe the interlocking of tusks in any of the zoos.

The use that the adult male babirusa makes of his canine teeth during agonistic behaviour remains incompletely known. Graafland (1898) suggested that the animals deliberately break their upper canines in order to make them better weapons. On the contrary, the evidence of the present study would indicate that the curved maxillary canine teeth are not used as weapons but as a shield preventing the lower tusks from reaching or deeply penetrating the opponent's body in most instances. With every upward thrust of the head towards the body of the opponent, it will be the curved upper tusks that first make contact with the opponent's body. The sole occasion that we witnessed one animal impaled on the lower canine of another was the result more of an accident than a deliberate attack. Indeed both animals seemed confused by the situation. The babirusa in Surabaya sometimes showed superficial scratch wounds on their shoulders, back and sides but we never saw how these were inflicted.

Ritualised fighting behaviours among other wild pigs have been divided into two categories; 1) frontal fighting involves head to head pushing and is shown by bush pig, warthog and giant forest hog and 2) lateral fighting which involves shoulder to shoulder pushing (either nose towards tail or head to head) is shown by wild boar (Frädrich 1965). The presence of elaborate tusks, and the wear pattern on the upper tusks of *B. b. babyrussa* have been interpreted as evidence that frontal fighting might be used by this subspecies (Frädrich 1965; MacKinnon 1981). Alternative explanations, such as the movement of stones and branches with the snout remain conceivable and may be preferable explanations



Fig. 7. The skull of an adult male babirusa (*Babyrousa babyrussa celebensis*) from Sulawesi (above) photographed and (below) X-rayed to demonstrate the shape, relative position and socket size of both the mandibular and maxillary canine teeth. Note that the socket of the maxillary canine tooth is significantly smaller than that of the mandibular canine

of wear when the relative fragility of the thinner canines in this subspecies is taken into account (Mohr 1960; Groves 1980). We believe that "boxing" may correspond to an additional category of pre-ultimate fighting behaviour in pigs. The "wrestling" described for *Sus scrofa cristatus* on Sri Lanka seems to fall within this third category (Barrette 1986).

The outstretched head and neck with the head lowered is one of the submissive postures shown by a range of ruminant artiodactyla as well as by all the wild pigs (Simpson 1964; Frädrich 1965; Ewer 1968; Cumming 1975; Seydack 1990). However, unlike wild boar, warthog, giant forest hog, and female babirusa, male babirusa do not run away in submission (Frädrich 1965; Cumming 1975; Kingdon 1989). Wild boar, warthog, bush pig, and babirusa all make a submissive noise when threatened or cornered (Frädrich 1965; Beuerle 1975; Cumming 1975; Seydack 1990). The noise made by the babirusa is similar to that described in detail for the wild boar (Klingholz et al. 1979; Briedermann 1990).

Fights between female warthog, bush pig, and giant forest hog were carried out in the same manner as between male animals (Frädrich 1965; Cumming 1975). In contrast, the agonistic behaviour of the female babirusa differs from that of the male in a number of significant ways. Most noticeably, the female bites with her incissors more actively than does the male. A female submits by holding her head close to the ground; in this way she both indicates submission and protects her lower limbs from being bitten. In addition, the submissive scream is more prevalent than in the male. Thirdly, the alpha female babirusa tends to be very aggressive and persistent, like the alpha female bush pig (Skinner et al. 1976; Seydack 1990); the inferior females seem to actively seek to avoid her attentions.

In the wild, agonistic behaviour of pigs is found in association with reproduction and with environmental resources such as food, water, nesting sites and hiding places. The amount, distribution and availability of these to the babirusa is presently unknown. It is therefore not yet possible, for example, to say whether this species exhibits a territorial claim on food, like the bush pig (Skinner et al. 1976; Seydack 1990), or not as shown by the wild boar, warthog and giant forest hog (Beuerle 1975; Cumming 1975; d'Huart 1978). It is likewise not clear whether or not babirusa in the wild engage in agonistic encounters within the context of territorial claim for mating partners and/or any of the other environmental resources. Additional studies, of home range, social organisation and habitat exploitation in the wild are required in order to answer these questions.

Acknowledgements

The hospitality shown by Pak Stany Subakir, Pak Bambang and Pak Vincent Harwono Gepak and the help and cooperation of the staff of the Kebun Binatang Surabaya is gratefully acknowledged. The interest shown by Dr. Linus Simanjuntak and his staff at Kebun Binatang Ragunan, Jakarta, and the cooperation of the staff at Antwerp and at the Jersey Wildlife Preservation Trust was much valued. The hospitality of Freifrau Ulla von Mengden and Pak Desianto was greatly appreciated. We acknowledge the help of Swaletreks for coordinating travel to Indonesia. Grateful thanks to the National Museums of Scotland for the loan of the babirusa skull (cat. no. 1989.073.061 – 0313) and Colin Warwick for photography. The financial support of the following organisations is gratefully acknowledged: Carnegie Trust for the Universities of Scotland; University of Edinburgh; Development Trust of the University of Edinburgh; Commission of the European Communities; Royal Zoological Society of Edinburgh; British Council; Wellcome Trust; James Rennie Bequest Fund; Weir Fund of the University of Edinburgh; Sir Stephen Watson Prize from the Edinburgh School of Agriculture; Duphar Veterinary Ltd.; Cotswold Pig Development Company Ltd.; Pig Improvement Company Ltd.; the Balloch Trust.

Zusammenfassung

Agonistisches Verhalten beim Hirscheber (Babyrousa babyrussa) in Gefangenschaft

An 95 Hirschebern aus Zoos von Indonesien, Belgien und den Kanalinseln wurden agonistische Verhaltenselemente in Abhängigkeit von Geschlecht, Körpergröße, Alter und Form der oberen Eckzähne untersucht. Insgesamt konnten 7 agonistische Verhaltensweisen erfaßt und beschrieben werden. Von diesen traten 3 regelmäßig in beiden Geschlechtern auf, 2 ausschließlich bei männlichen Individuen und 2 weitere hauptsächlich bei Männchen, gelegentlich aber auch bei Weibchen. Unterwerfung wurde stets durch gesenkten Kopf und besondere Lautäußerungen signalisiert. Die Eckzähne wurden nie als Waffen eingesetzt. Die Verhaltensweise "Boxen" ist typisch für Auseinandersetzungen zwischen männlichen Individuen, wohingegen weibliche Tiere stets versuchen, in die Vorderläufe der Gegnerin zu beißen. Adulte Weibchen waren gegenüber adulten Männchen unterwürfig, aber gegenüber sub-adulten Männchen dominant. Große Weibchen waren auch dominant gegenüber kleineren.

References

Barrette, C. (1986): Fighting behaviour of wild *Sus scrofa*. J. Mammalogy **67**, 177–179.

Beuerle, W. (1975): Freilanduntersuchungen zum Kampf- und Sexualverhalten des europäischen Wildschweines (*Sus scrofa* L.). Z. Tierpsychol. **39**, 211–258.

Bowles, D. (1986): Social behaviour and breeding of babirusa (*Babyrousa babyrussa*) at the Jersey Wildlife Preservation Trust. Dodo **23**, 86–94.

Briedermann, L.(1990): Schwarzwild. 2nd ed. Berlin: VEB Deutscher Landwirtschaftsverlag.

Cumming, D. H. M. (1975): A Field Study of the Ecology and Behaviour of Warthog. Mus. Mem. **7**, 1–179.

d'Huart, J. P. (1978): Ecologie de l'hylochere (*Hylochoerus meinertzhageni* Thomas) au Parc National des Virunga, Zaire. Fondation pour favoriser les recherches scientifiques en Afrique, 2e Serie, fasc. **25**, 1–156.

Ewer, R. F. (1968): Ethology of Mammals. London: Logos Press.

Frädrich, H. (1965): Zur Biologie und Ethologie des Warzenschweines (*Phacochoerus aethiopicus* Pallas), unter Berücksichtigung des Verhaltens anderer Suiden. Z. Tierpsychol. **22**, 328–393.

— (1967): Das Verhalten der Schweine (Suidae, Tayassuidae) und Flußpferde (Hippopotamidae). Hb. Zool. VIII, 10. Teil **26**, 1–44.

Geist, V. (1966): The evolution of horn-like organs. Behaviour **27**, 175–214.

Geoffroy-St-Hillaire, T. E.; Cuvier, F. (1842): Histoire naturelle des mammiferes. Paris: Blaise Vol. 7, 1–4.

Graafland, N. (1898): De Minahassa. 2nd ed. Batavia: G. Kolff. Part 2.

Groves, C. P. (1980): Notes on the systematics of *Babyrousa*. Zool. Meded. **55**, 29–46.

Heinsius, H. W.; Vogt, A. F. W. (1916): Wilde dieren naar het leven. Amsterdam. Pp. 209–210.

Kingdon, J. (1989): East African Mammals: an Atlas of Evolution in Africa. Chicago: The University of Chicago Press. Vol. IIIB, pp. 184–249.

Klingholz, F.; Siegert, C.; Meynhardt, H. (1979): Die akustische Kommunikation des Europäischen Wildschweines (*Sus scrofa* L). Zool. Garten. N. F. **49**, 277–303.

Leus, K.; Bowles, D.; Bell, J.; Macdonald, A. A. (1992): Behaviour of the babirusa (*Babyrousa babyrussa*) with recommendations for its husbandry. Acta Zool. Pathol. Antverpiensia **82**, 9–27.

Macdonald, A. A.; Bell, J.; Munro, S. A.; Kaspe, L.; Harwono Gepak, V.; Sasmita, R.; Bowles, D. (1989): Observations on the behaviour and health of captive babirusa. In: Proc. Simp. Nasional Penyakit Satwa Liar, Surabaya, Indonesia: Univ. Airlangga dan Kebun Binatang. Pp. 244–253.

MacKinnon, J. (1981): The structure and function of the tusks of babirusa. Mammal Rev. **11**, 37–40.

Maynard Smith, J. (1982): Evolution and the Theory of Games. Cambridge: University Press.

Mohr, E. (1960): Wilde Schweine. Die Neue Brehm-Bücherei. No. 247. Wittenberg Lutherstadt: Ziemsen.

Patry, M. (1990): Babiroussa: une vie jusqu'au bout du reve. Paris: Fixot.

Patry, M.; Capiod, J. (1989): Pour la premier fois le Babiroussa a l'etat naturel. Connaissance de la Chasse **156**, 45–46.

Schaftenaar, W. (1991): Treatment of a fractured tusk in a male babirusa (*Babyrousa babyrussa*) using a polyoxymethylene bolt. J. Zoo Wildl. Med. **22**, 364–366.

Selmier, V. J. (1978): Only in Indonesia-The Babirusa. Jakarta, Indonesia: Lembaga Ilmu Pengatahuan Indonesia.

— (1983): Bestandsgröße und Verhalten des Hirschebers (*Babyrousa babyrussa*) auf den Togian Inseln. Bongo **7**, 51–64.

Seydack, A. H. W. (1990): Ecology of the Bushpig *Potamochoerus porcus* Linn., 1758 in the Cape Province, South Africa. PhD thesis. Univ. Stellenbosch.

Simpson, C. D. (1964): Observations on courtship behaviour in warthog *Phacochoerus aethiopicus* Pallas. Arnoldia **1**, 1–4.

Skinner, J. D.; Breytenbach, G. J.; Maberly, C. T. A. (1976): Observations on the ecology and biology of the bushpig *Potamochoerus porcus* Linn. in the Northern Transvaal. S. Afr. J. Wildl. Res. **6**, 123–128.

Whitten, A. J.; Mustafa, M.; Henderson, G. S. (1987): The ecology of Sulawesi. Yogyakarta: Gadja Mada University Press. Pp. 414–418.

Authors' addresses: Alastair, A. Macdonald and Kristin Leus, Department of Preclinical Veterinary Sciences, The Royal (Dick) School of Veterinary Studies, The University of Edinburgh, Summerhall, Edinburgh EH9 1QH, Scotland UK; David Bowles, Environmental Investigation Agency Ltd., 208/209 Upper Street, London N1 1RL, England, UK; and Justine Bell, Centre de Recherche en Reproduction Animale, Faculte de Medecine Veterinaire, Universite de Montreal, 3200 Rue Sicotte, CP 5000, St.-Hyacinthe, Quebec, Canada J2S 7C6

Z. Säugetierkunde 58 (1993) 31–37

ISSN 0044-3468

Influence of the hormonal state of female Mongolian gerbils (*Meriones unguiculatus*) on urinary chemosignals stimulating scent-marking behaviour of males

By B. Probst and Heidrun Schönheiter

Zoologisches Institut/Tierphysiologie der Universität Tübingen, Tübingen, FRG; und Lehrstuhl Tierphysiologie der Universität Bayreuth, Bayreuth, FRG

Receipt of Ms. 24. 2. 1992
Acceptance of Ms. 6. 4. 1992

Abstract

Investigated the influence of urine from female Mongolian gerbils (*Meriones unguiculatus*) at different endocrine conditions on urinary chemosignals that stimulate male scent-marking behaviour. The scent-marking behaviour of male Mongolian gerbils is increased by presence of females. This increase is mediated by non-volatile polypeptides excreted in urine by mature females. In the present study the scent-marking behaviour stimulating efficacy of female urine originating from ovariectomized and hormone-treated females and also from mature females during different estrous states was determined. Urine from ovariectomized females and ovariectomized females treated only with progesterone did not increase the scent-marking frequencies of males in the open-field tests. After treatment of ovariectomized females with estradiol or estradiol together with progesterone female urine significantly stimulated the scent-marking frequencies of males. The natural estrous cycle of Mongolian gerbils appeared rather unpredictable in individual females, while 4–6 day intervals were dominating in the complete sample. Only urine from proestrous females stimulated scent-marking behaviour of males while urine from other estrous states was ineffective.

Introduction

Fertile male Mongolian gerbils (*Meriones unguiculatus*) display an androgen-dependent scent-marking behaviour (Thiessen 1968), during which they deposit the secretions from a specialized ventral scent gland onto prominent objects in their environment. In fertile males the frequency of this scent-marking behaviour is highly dependent on the availability of chemical signals excreted by females (Probst 1985a). Based upon that increase in scent-marking frequency we developed a bioassay for the chemical signal: Males kept without females scent-mark on a low basal level that is approximately doubled when female urine or an appropriate test sample is applied to the nares of the males (Probst and Lorenz 1987).

Mature female gerbils undergo a spontaneous estrous cycle of 4 to 7 days (Marston and Chang 1965; Barfield and Beeman 1968; Vick and Banks 1969). The present experiments therefore investigated the influence of the sexual status of the donor females on the scent-marking stimulating efficacy of their urine. Tested were urine samples from ovariectomized females with and without hormone treatment, and from intact females at different states of their estrous cycle.

Material and methods

Animals and housing

Mongolian gerbils (*Meriones unguiculatus*) were obtained from our breeding colony. Males were housed in individual macrolon cages with wire mesh tops (cage size: 37 × 20 × 15 cm). Females were

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5801-0031 $ 02.50/0

kept in groups of two or three per cage. All gerbils were maintained on a 12:12 hours light-dark cycle (lights on from 02.00 to 14.00 hours) with constant room temperature (22 ± 1 °C) and relative humidity (55 %). Gerbil food pellets (Altromin, Lage, Germany) and tap water were available ad lib.

Behavioural observation

The experimental males were kept in a separate room where only males were present. Their scent-marking behaviour was observed daily in the same room in an open-field apparatus (Thiessen 1968), modified as described earlier (60 × 60 cm, transparent walls 27 cm, 9 marking pegs; Probst 1985b). For scent-marking tests, individual males were placed inside this open-field and all occurrences of scent-marking behaviour during 5 minutes were counted. All observations were made during the third hour of the dark phase of the light-dark cycle. A dimmed fluorescent bulb provided sufficient illumination for observation of the animals after a short period of adaptation.

Bioassay procedure

To determine the efficacy of different urine samples to increase scent-marking activity, each male received 20 μl of the respective urine sample onto its nares twice per day. The samples were given at least 7 hours before the behavioural tests and immediately following the tests. Evaluated were 3 trials per male starting after 5 days of urine treatment. The stimulating effect of female urine on male scent-marking behaviour is completely vanished after 2 weeks without treatment. Between different treatments a phase of 7 to 18 days with no treatment was placed, during that the decline of scent-marking activity back to the basal level was monitored. This experimental design allowed us to compare marking activities from the same males under different experimental conditions thus avoiding the comparison between different treatment groups. At the start and after completion of an experiment all males were tested with pooled female urine to verify that no habituation of the response had occurred during the series.

Statistical analysis

The basal and pooled urine stimulated marking activities determined at the start and after the respective experiment were compared using Wilcoxon matched-pairs signed-ranks test. Since there were no significant differences (Tab. 1), all basal marking activities during the tests were averaged to one individual's basal marking activity. In addition, the response to pooled urine is not significantly different at the start compared to the end of the experiment (Table). For further statistical analyses, the average scent-marking activity during the respective treatment period was computed for every male. The effects of different treatments in both experiments were then evaluated by parametric analysis of variance (ANOVA), because Bartlett (Chi^2 [df = 4] = 6.65 and 2.02) and Hartley (F-max [df = 4] = 2.29 and 1.87) tests indicated homogeneity of variances ($p = 0.15$ and 0.75). When applicable, significant treatment effects were evaluated using the Tukey honest significant difference (HSD) test. Interactions between consecutive tests were prevented by the randomized treatment sequence and the intermediate unstimulated period, during that the decline of marking activities to the basal level was monitored. The significance level was set to $p < 0.05$.

Experiment 1: Influence of urine from ovariectomized and hormone-treated females

Nine adult females were ovariectomized under Ketanest (Parke, Davies and Co., Berlin, Germany) anesthesia. Starting six weeks after surgery urine was collected from these females (OVX) by placing

Comparison of basal and pooled urine stimulated marking activities (mean ± SEM) obtained at the start (no. 1) and the end (no. 2) of the respective experiment

NS indicates not significantly different marking activities using Wilcoxon matched-pairs signed-ranks test ($p > 0.05$)

	Experiment 1 (N = 15)		Experiment 2 (N = 15)	
Basal no. 1	8.52 ± 1.06	NS	15.28 ± 2.01	NS
Basal no. 2	8.53 ± 1.07		14.87 ± 2.29	
Pool no. 1	14.98 ± 1.45	NS	27.24 ± 3.05	NS
Pool no. 2	15.47 ± 1.45		27.82 ± 2.95	

every female individually inside a beaker for some minutes. Following this sampling period, the females were randomly assigned to one of three groups. One group (E2) received estradiol benzoate for 10 days (5μg once per day). Another group (P) received progesterone for ten days (0.5 mg once per day). Urine was collected on days 5 to 10 of hormone treatment in E2 and P groups. The last group (E2 + P) was treated with estradiol (5 μg; 48 and 24 before sampling) and progesterone (0.5 mg; 3 hours before sampling); this treatment reliably elicited receptive behaviour.

Individual urine samples were kept frozen at −40 °C until the end of the sampling period, when urine from equal treatment groups was pooled. Fifteen experimental males received these pooled urine samples in randomly assigned sequence.

Experiment 2: Influence of urine from different natural estrous states

Twentysix females, 6–7 months of age, were used as urine donors. For daily urine collection, every female was individually placed inside a beaker for a maximum of 2 minutes. The urine sample was collected and immediately stored frozen at −40 °C. Subsequently the estrous state of this female was determined by placing her inside the cage of a sexually active male. A female was rated in behavioural estrus when the male caused the display of lordosis behaviour (Davies et al. 1974; Burley 1980). Immediately after the estrous state was determined, the female was removed from the male to prevent pregnancies during the experiments.

After completion of the sampling period (103 days) the urine samples from all females were classified according to the following estrous states:

DE = diestrus: no receptive behaviour at least one day before and one day after this sampling day
PE = proestrus: the day before behavioural estrus was observed
E = estrus: the female was receptive and displayed lordotic behaviour
ME = metestrus: the day following behavioural estrus

The pooled urine samples of the above classes were dialysed against demineralized water for 1 hour, which reduced osmolarity from more than 3000 mosmol/l to 200 mosmol/l (Knaur Micro-Osmometer, Knauer, Germany) to prevent any possible impairment of the nasal mucosa during the experiments.
Fifteen males were testes in randomized sequence with urine from the different estrous states.

Results

Experiment 1: The scent-marking activities of the 15 test males remained unaffected during treatment with urine from ovariectomized female conspecifics (Fig. 1). Also, urine from ovariectomized females treated with progesterone failed to stimulate male scent marking

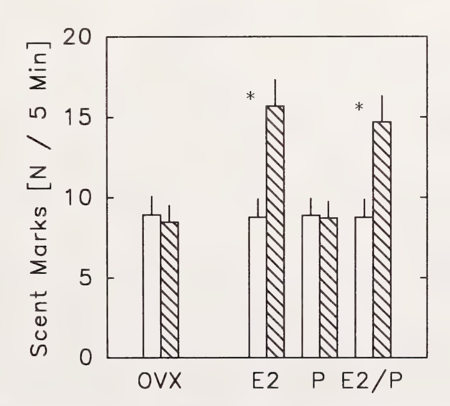


Fig. 1. Influence of urine from ovariecomized females (OVX) and females treated with progesterone (P), estradiol (E2) or progesterone and estradiol (E2/P) on male marking activity. Indicated is the basal marking activity (open columns) and the marking activity after at least 5 days of urine treatment (striped columns) (mean ± SEM, n = 15, *: $p < 0.01$)

behaviour. Urine from ovariectomized females treated daily with estradiol or with a combination of estradiol (HSD: $p < 0.01$) and progesterone (HSD: $p < 0.02$) significantly increased the scent marking levels of the males (ANOVA: F [4; 70] = 7.4; $p < 0.001$).

Experiment 2: A total of 109 cycles were observed in the 26 females (2–8 cycles per female). Cycles with 4 to 6 days of length clearly dominated with more than 75 % of all cycles observed. However, 7 females displayed anestrous periods from 7 to 23 days of length. Urine from such anestrous periods was not used for stimulation of the males.

Analysis of variance for the scent-marking activities revealed a statistically significant difference in scent-marking response to urine from different estrous states (ANOVA: F [4;70] = 4.07, $p < 0.001$). Post-hoc comparisons showed that urine from proestrous females significantly increased male scent-marking activities (HSD: $p < 0.05$; Fig. 2). There was no significant influence of estrous, metestrous and diestrous urine on male scent-marking frequency.

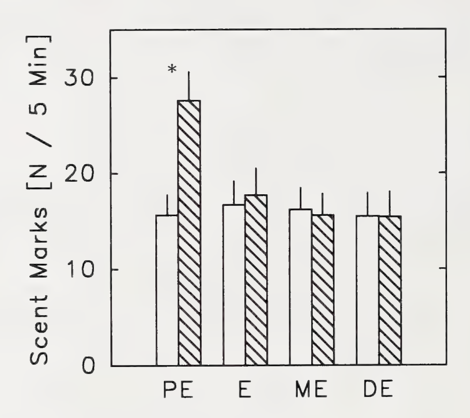


Fig. 2. Influence of urine from intact females in different estrous states on male marking activity. Indicated is the basal marking activity (open columns) and the marking activity after at least 5 days of urine treatment (striped columns) (mean ± SEM, n = 15, *: $p < 0.01$). PE = proestrus, E = estrus, ME = metestrus, DI = diestrus

Discussion

The experiments reported here investigated the influence of the sexual state of females on the efficacy of their urine to increase the scent-marking activities of male conspecifics. During the first experiment the sexual status of the females was manipulated using ovariectomized and hormone-treated females. For the second experiment urine was obtained from mature females having a natural estrous cycle. Effects of the endocrine and sexual condition of the female urine donors on the males' scent-marking activities were found in both experiments.

In a number of experiments before starting these series, we evaluated different methods for determination of female receptivity. The typical sequence of different cell types found in vaginal smears during the estrous cycle in other rodents [rat *Rattus norvegicus*]: Long and Evans 1922; hamster (*Mesocricetus auratus*): Kupperman 1944; Scharmann et al. 1988; mouse (*Mus musculus*): Bronson et al. 1966) was not observed in gerbils (see also Marston and Chang 1965). The change of cell types in vaginal smears, therefore, cannot predict the day of estrus in gerbils. Also, the urinary excretion of free estradiol did not show the cyclic pattern (Fenske and Probst, data not shown) that can be found in other female mammals during the ovarian cycle (Bonney and Setchell 1980; Khatkatay et al.

1988; Härter and Erkert 1991). The hormonal regulation of the chemical signal by estradiol as found in experiment 2 is not detectable as a rhythmic pattern of the excreted amount of estradiol in cycling females. However, the estradiol metabolites in the urine were not determined in the present study. Therefore, the regulatory function of estradiol in cycling females can not be rejected by this method. In the present study the intervals between consecutive heats were unpredictable in individual females. This is in contrast to Burley et al. (1980), who observed rather constant 4 day cycles in individual females. Therefore, daily pairing with a sexually active male, which proved to be the most reliable determination of the estrous state, was performed throughout the experiments. These sexually active males usually responded to female receptive behaviour in less than 60 seconds with sexual behaviour.

Sexual and endocrine conditions exert effects on behaviour in various species. Male golden hamsters (*Mesocricetus auratus*) flank marked at low rates in soiled cages of females on estrous and one day postestrous, and at high rates when females were on non-estrous days (Johnston 1977). The effect of the endocrine condition of the female on male behaviour in direct encounters was also investigated by Agren and Meyerson (1977). In their study, male Mongolian gerbils (*Meriones unguiculatus*) displayed most marking when females were ovariectomized and not treated with hormones, while estradiol-treated females as well as estradiol- and progesterone-treated females elicited only 50 % of the marking scores as compared to the untreated females. In our experiments, female urine stimulated male scent-marking activity when females were one day before estrous or when ovariectomized females were treated with estradiol or a combination of estradiol and progesterone. The effect on scent-marking, however, is not comparable between these studies. Agren and Meyerson (1977) as well as Johnston (1977) observed an immediate change in the behaviours displayed during an encounter or under changing experimental conditions. During the treatment of male gerbils with female urine their scent-marking activities do not increase immediately (Probst 1985a). After at least three days of continuous treatment the scent-marking activities achieve a higher level. This higher level is maintained after withdrawal of the stimulus for one or two days. It then takes several days until the marking levels steadily decrease back to the basal marking activities. This means, the internal mechanism that sets the marking activity of a male to a specific level is modulated by the chemical signals from urine of proestrous females. Using the terminology for the classification of pheromones (Vandenbergh 1983) for these experiments (Agren and Meyerson 1977; Johnston 1977), the immediate changes in specific behaviours would be caused by "signalling pheromones". In contrast to that, the long-lasting increase in marking activity induced by urinary chemosignals in male gerbils would be caused by "primer pheromones". In contrast to the effects of other primer pheromones, female urine causes a reversible increase of scent-marking behaviour in male gerbils, and not an irreversible developmental or morphological change (Vandenbergh et al. 1975; Drickamer 1986).

Although the physiological control of scent-marking behaviour is well known in gerbils (Thiessen and Yahr 1977) the biological functions of this behaviour are still unclear (Baran and Glickman 1970; Fullenkamp et al. 1985). The increased marking frequency could provide olfactory familiarity of a particular male that functions to mitigate a female's aggressiveness during encounters (Daly 1977). In a recent field study from Inner Mongolia, Agren et al. (1989) found 6–8 times more marking behaviour during sexual interactions than before. As demonstrated by the present results, the efficacy of female urine to increase scent-marking in males depends on the sexual state of the female. This all indicates an important function of male scent-maring behaviour in the sexual context.

Acknowledgements

This work was supported by a grant of Deutsche Forschungsgemeinschaft (Pr 285/1-1) to B. P. We thank SÜNJE MEYER and DANIELA HIRZEL for help during the experiments.

Zusammenfassung

Einfluß des hormonellen Status weiblicher Mongolischer Rennmäuse (Meriones unguiculatus) auf die Steigerung des Markierverhaltens von Männchen durch chemische Signale im Urin

Untersucht wurde, welchen Einfluß des Sexualstatus von weiblichen Mongolischen Rennmäusen (*Meriones unguiculatus*) auf im Urin enthaltene chemische Signale hat, die das Markierverhalten von Männchen steigern. Die Häufigkeit des Markierverhaltens von männlichen Mongolischen Rennmäusen wird durch die Gegenwart von Weibchen gesteigert. Dieser Anstieg wird durch schwerflüchtige Polypeptide bewirkt, die mit dem Urin fertiler Weibchen ausgeschieden werden. Für diese Untersuchungen wurde Urin von ovarektomierten und hormonbehandelten Weibchen sowie Urin aus bestimmten Ovarialzyklusphasen von fertilen Weibchen gesammelt. In einem Biotest wurde anschließend bestimmt, inwieweit diese Urinproben die Markieraktivität von Männchen steigern können. Urin ovarektomierter Weibchen und von ovarektomierten Weibchen bei Behandlung mit Progesteron führte dabei zu keiner Steigerung der Markieraktivität. Wurden ovarektomierte Weibchen mit Östradiol oder Östradiol und Progesteron behandelt, so führte ihr Urin zu einer signifikanten Zunahme der Markieraktivität bei Männchen. Die Zykluslänge war bei einzelnen Weibchen sehr variabel, obwohl insgesamt 4–6 Tage lange Zyklen vorherrschten. Nur der Urin proöstrischer Weibchen führte zu einer signifikanten Steigerung der Markieraktivität, während Urin der anderen Östrusstadien unwirksam war.

References

AGREN, G.; MEYERSON, B. J. (1977): Influence of gonadal hormones and social housing conditions on agonistic, copulatory, and related socio-sexual behaviour in the Mongolian gerbil (*Meriones unguiculatus*). Behav. Process. **2,** 265–282.

AGREN, G.; ZHOU, Q.; ZHONG, W. (1989): Ecology and social behaviour of Mongolian gerbils, *Meriones unguiculatus,* at Xilinhot, Inner Mongolia, China. Anim. Behav. **37,** 11–27.

BARAN, D.; GLICKMAN, S. E. (1970): "Territorial marking" in the Mongolian gerbil: A study of sensory control and function. J. Comp. Physiol. Psychol. **71,** 237–245.

BARFIELD, M. A.; BEEMAN, E. A. (1968): The oestrous cycle in the Mongolian gerbils, *Meriones unguiculatus.* J. Reprod. Fertil. **17,** 247–251.

BONNEY, C. R.; SETCHELL, K. D. R. (1980): The excretion of gonadal steroid during the reproductive cycle of the owl monkey (*Aotus trivirgatus*) J. Steroid. Biochem. **12,** 417–421.

BRONSON, F. H.; DAGG, C. D.; SNELL, G. D. (1966): Reproduction. In: The biology of the Laboratory Mouse. Ed. by L. L. GREEN. New York: McGraw-Hill.

BURLEY, R. A. (1980): Pre-copulatory and copulatory behaviour in relation to stages of the oestrous cycle in the female Mongolian gerbil. Behaviour **72,** 211–241.

DALY, M. (1977): Some experimental tests of the functional significance of scent-marking by gerbils (*Meriones unguiculatus*). J. Comp. Physiol. Psychol. **91,** 1082–1094.

DAVIES, H. N. JR.; ESTEP, D. Q.; DEWSBURY, D. A. (1974): Copulatory behavior of Mongolian gerbils (*Meriones unguiculatus*). Anim. Learn. Behav. **2,** 69–73.

FULLENKAMP, A.; FISHER, R. B.; VANCE, R. A.; DUFFEY, K. A. (1985): The failure to demonstrate avoidance of ventral gland odors in male Gerbils (*Meriones unguiculatus*). Physiol. Behav. **35,** 763–765.

HÄRTER, L.; ERKERT, H. G. (1991): The length of the ovarian cycle does not depend on the circadian period length on common marmosets, *Callithrix j. jacchus.* In: Primatology today. Ed. by A. EHARA, T. KIMURA, O. TAKENAKA, and M. IWAMOTO. Amsterdam: Elsevier Science Publishers. Pp. 431–434.

JOHNSTON, R. E. (1977): Scent marking by male Golden hamsters (*Mesocricetus auratus*). Z. Tierpsychol. **37,** 75–98.

KHATKHATAY, M. I.; SANKOLLI, G. M.; MEHERJI, P, K.; CHOWDHURY, V.; JOSHI, U. M. (1988): Excretion of estrone-3-glucuronide in urine in spontaneous and induced ovulatory cycles. Int. J. Fertil. **333,** 181–187.

KUPPERMAN, H. S. (1944): Sexual cycle and dimorphic pigmentation in the golden hamster (*Cricetus auratus,* Waterhouse). Endocrinology **35,** 225.

LONG, J. A.; EVANS, H. M. (1922): The oestrous cycle in the rat and its associated phenomena. Mem. Univ. Calif. **6,** 1–148.

MARSTON, J. H.; CHANG, M. C. (1965):The breeding, management and reproductive physiology of the Mongolian gerbil (*Meriones unguiculatus*). Lab. Anim. Care **15,** 34–48.

PROBST, B. (1985a): Female urinary chemosignals influence scent-marking behaviour in male Mongolian gerbils (*Meriones unguiculatus*). Z. Naturforsch. **40c**, 936–938.
— (1985b): Individual marking activities not reflected by respective testosterone levels in male gerbils. Physiol. Behav. **34**, 363–367.
PROBST, B.; LORENZ, M. (1987): Increased scent marking in male Mongolian gerbils by urinary polypeptides of female conspecifics. J. Chem. Ecol. **13**, 851–861.
SCHARMANN, W.; NAGEL, P.; HELLER, A. (1988): Oestrus phases of the Syrian hamster. Z. Versuchstierkde. **31**, 276–280.
THIESSEN, D. D. (1968): The roots of territorial marking in the Mongolian gerbil: A problem of species-common topography. Behav. Res. Meth. Instru. **1**, 70–76.
THIESSEN, D. D.; YAHR, P. (1977): The gerbil in behavioural investigations. Austin: University of Texas Press.
VANDENBERGH, G. H. (1983): Pheromones and Reproduction in Mammals. New York: Academic Press.
VANDENBERGH, G. H.; WHITSETT, J. M.; LOMBARDI, J. R. (1975): Partial isolation of a pheromone accelerating puberty in female mice. J. Reprod. Fertil. **43**, 515–523.
VICK, L. H.; BANKS, E. M. (1969): The oestrous cycle and related behaviour in the Mongolian gerbil (*Meriones unguiculatus* Milne-Edwards). Comm. Behav. Biol. **3**, 117–124.

Authors' addresses: Dr. BODO PROBST, Zoologisches Institut, Tierphysiologie, Universität Tübingen, Auf der Morgenstelle 28, D-7400 Tübingen, FRG; Dipl.-Biol. HEIDRUN SCHÖNHEITER, Lehrstuhl Tierphysiologie, Universität Bayreuth, D-8580 Bayreuth, FRG

Z. Säugetierkunde 58 (1993) 38–47

ISSN 0044-3468

Le cycle sexuel chez le mulot sylvestre, *Apodemus sylvaticus* (L., 1758), (Muridae) en région méditerranéenne

Par R. Fons et Marie Charlotte Saint Girons

Laboratoire Arago, Université P. et M. Curie et CNRS, U.R.A. 117, Banyuls-sur-Mer, et Laboratoire d'Evolution des Etres Organisés Paris, France

Réception du Ms. 9. 1. 1992
Acceptation du Ms. 20. 5. 1992

Abstract

Reproductive cycle of the long-tailed field mouse, Apodemus sylvaticus (L., 1758), (Muridae) in the Mediterranean area

Data on 1301 long-tailed field mice, *Apodemus sylvaticus,* have been collected in the Mediterranean area. Their sexual cycle was studied in the wild. They were compared with data from Britanny and Northern Africa. A special section is devoted to Corsica. Start and length of the sexual activity appear to be very variable. In mid Europe and on Mediterranean mountains, wild long-tailed field mice are sexually active from early spring to late autumn. There is no sexual activity during the winter season. On the contrary, in Mediterranean coastal areas and islands, the sexual activity takes place during the winter and the pause during the summer. In the wild, other murides (*Rattus rattus, Mus musculus* and *M. spretus*) don't show comparative adaptation of their sexual cycle. They have the same rhythm in the entire Western part of their distribution. In the Mediterranean area, *Apodemus sylvaticus* shows a remarkably well suited, strategical answer to the availability of food which itself depends on the climatic conditions.

Introduction

Certaines espèces de mammifères ont une valence écologique particulièrement accentuée. Il est fréquent, par exemple, qu'une espèce carnivore adapte son régime alimentaire à l'éventail des proies disponibles et ajuste son rythme circadien d'activité de façon à éviter ses prédateurs ou ses compétiteurs. Le déterminisme du cycle sexuel et l'adaptation de la période d'activité sexuelle aux contraintes différentes de leur environnement semblent plus rares, ou moins bien étudiés, du moins chez les rongeurs. C'est le cas, en particulier, pour le mulot sylvestre, *Apodemus sylvaticus,* taxon bien connu pour ses capacités adaptatives. Ce rongeur est très largement répandu en Europe et occupe également une partie de l'Afrique du Nord. Or, les données concernant la période d'activité sexuelle des adultes sont contradictoires. Ayant pu observer cette espèce au Maroc, dans les îles méditerranéennes, dans les Pyrénées-Orientales, en Bretagne et dans la Région Parisienne, nous avons rassemblé nos données relatives à la reproduction en les comparant à celles fournies par la bibliographie afin d'essayer de comprendre ces divergences.

Matériel et méthodes

Pour les individus en provenance d'Afrique du Nord et de France continentale, nous disposions surtout d'animaux morts pour lesquels l'état sexuel a été déterminé par dissection. En zone méditerranéenne continentale et insulaire, la majorité des renseignements proviennent d'animaux vivants, immédiatement relâchés (plan-quadrat, ligne standard de piégeage).

Sur les quadrats (continent et Corse), les pièges ont été disposés par 2 selon une grille à maille de 20 mètres matérialisée par des jalons. Après une inspection attentive, les animaux marqués par amputation de phalangettes selon un code préétabli, sont relâchés le plus rapidement possible à leur point de

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5801-0038 $ 02.50/0

capture. L'effort de piégeage est poursuivi jusqu'à ce que 70 à 80 % des animaux capturés soient marqués. Ce résultat est obtenu après 3–4 jours consécutifs de piéggeage en moyenne. Les lignes standard comprennent 55 pièges de plusieurs modèles (grillagés type Firobin, INRA, Sherman) disposés tous les 3 m au moins soit une longueur totale de 160 à 180 m. Le piégeage dure 3 jours (72 heures consécutives) avec un relevé toutes les 24 heures. Afin d'apprécier l'impact de l'incendie sur les populations de micromammifères (Fons et al. 1988) des piégeages ont été effectués dans divers milieux méditerranéens continentaux (pelouses, maquis, chênaies) durant six années consécutives. Nous ne gardons dans cette étude que les observations faites dans les zones proches et intactes, utilisées comme témoins. L'influence du feu sur la structure des populations étant accentuée, tous les animaux capturés sur brûlis sont exclus. Au contraire, les résultats fournis par l'étude d'un quadrat établi depuis plusieurs années en Corse sur une guilde de micromammifères ont pu être tous comptabilisés. Enfin, de nombreux piégeages complémentaires ont été effectués en Corse et dans les Pyrénées-Orientales.

Résultats

Cycle sexuel chez *Apodemus sylvaticus*

Bretagne

Il s'agit d'une zone de bocage, en climat atlantique, située à 30 kilomètres au nord de Nantes. Certains résultats ont été publiés précédemment (Saint Girons 1955; Le Louarn et Saint Girons 1977; Saint Girons et Wodzicki 1985). Le pourcentage des jeunes dans la population se répartit comme l'indique la figure 1. Si l'on admet que les jeunes sont âgés d'un mois environ au moment où ils apparaissent dans les piégeages, les premières naissances ont lieu en février; la période d'activité sexuelle se poursuit jusqu'en octobre et s'arrête à la fin de l'automne. Des reproductions d'hiver ne sont cependant pas exceptionnelles.

Le cycle sexuel des mâles a été étudié par examen des testicules, Leur poids varie d'une quarantaine de milligrammes fin automne – début de l'hiver jusqu'à 800 mg en moyenne en juin. La période de reproduction débute donc à la fin de l'hiver et se termine en septembre–octobre chez les mâles.

Chez les femelles, on trouve des individus en gestation de février à septembre. Les premières femelles lactantes apparaissent en mars. Le nombre des femelles en lactation dépasse sensiblement celui des femelles gravides en août et septembre. Le repos sexuel se

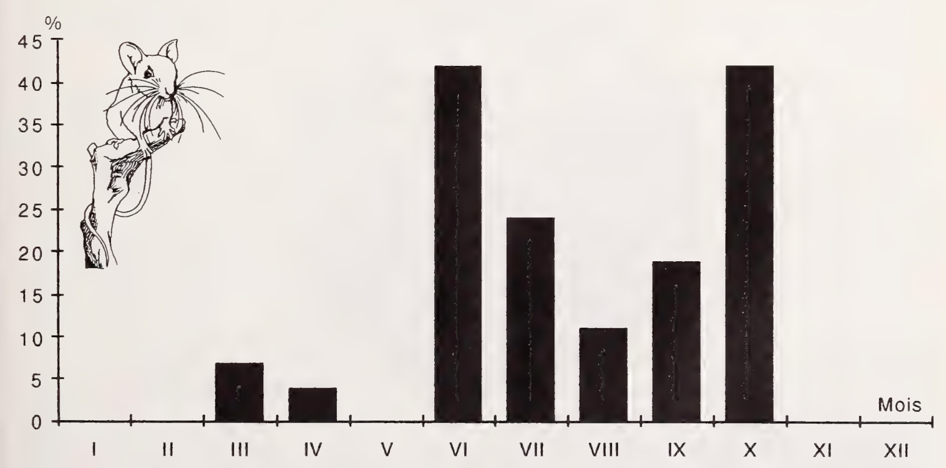


Fig. 1. Pourcentage des jeunes dans la population aux divers mois de l'année en Haute Bretagne chez *Apodemus sylvaticus*

poursuit d'octobre à mars et les quelques portées d'hiver pourraient être mises en liaison avec les conditions climatiques particulièrement favorables influant sur la nourriture disponible.

Pour l'ensemble de la population, il y a deux pics dans l'intensité de l'activité sexuelle, l'un en mai–juin, l'autre en septembre. Le maximum de densité des populations apparaît à la fin de l'été ou au début de l'automne.

Région Parisienne

Dans un parc du département de l'Essonne (sud de Paris), les modalités de la reproduction sont sensiblement les mêmes qu'en Bretagne mais l'activité sexuelle débute plus tard et se poursuit plus longtemps. Les jeunes ne sont absents des piégeages qu'en février et mars et on en trouve encore de nombreux représentants en novembre et décembre. On observe encore en mars des femelles adultes au repos sexuel bien que, dès le mois de janvier, les dimensions des testicules des mâles adultes commencent à croître.

Pyrénées-Orientales

Des mulots ont été capturés dans la région de Banyuls-sur-Mer en septembre 1955, tant au niveau de la mer qu'entre 700 et 900 mètres, dans une forêt de hêtres (*Fagus sylvatica*), (Réserve naturelle de la Massane) (Saint Girons 1957). Au niveau de la mer, dans des roselières et des buissons bordant un ruisseau à sec, les mâles présentent des testicules gonflés mais chez quelques individus ils se trouvent dans la cavité abdominale. 60 % des femelles sont en repos sexuel. Au contraire, dans la forêt de hêtres de basse altitude, tous les mâles sont en activité sexuelle ainsi que 62 % des femelles. Les nombreux piégeages effectués régulièrement tant dans différents milieux du biome méditerranéen que dans la Réserve de la Massane le confirment (Herrenschmidt 1978; Torregrosa Orts et al. 1987).

Plus récemment, des captures (1301 individus) ont été effectuées dans l'étage mésoméditerranéen (sensu Quezel 1974) des Pyrénées-Orientales. Il s'agit de la partie altitudinale où les groupements forestiers sont dominés par les chênes à feuilles persistantes: chênes-lièges (*Quercus suber*) et chênes verts (*Q. ilex*). Les deux secteurs sont localisés dans le massif des Aspres, Piedmont du Canigou et dans la chaîne des Albères, située à l'extrémité de la zone axiale pyrénéenne qui se termine brutalement sur la Méditerranée. Ils ont permis de suivre l'évolution de la structure des populations au cours de plusieurs cycles successifs (Fons et al. 1988).

En subéraies préservée du feu, des piégeages poursuivis pendant 6 ans montrent que le cycle sexuel du mulot est complètement inversé par rapport à celui mis en évidence dans le bocage atlantique. Le repos sexuel est estival et la période de reproduction maximale se place en hiver. En juillet 1979, les adultes sont au repos sexuel et les jeunes absents. En février 1980, la proportion de jeunes est au contraire très importante et témoigne d'une activité sexuelle d'hiver. Un tel schéma s'est poursuivi au cours des années suivantes. La figure 2 A montre les pourcentages mensuels d'adultes des deux sexes en activité sexuelle lors des différentes sessions de piégeages. Jointe aux données fournies par l'apparition des jeunes dans les pièges, cette figure met en évidence une activité sexuelle moyenne au printemps, un repos estival qui peut affecter toute la population en juillet et août et une forte reprise de l'activité sexuelle en automne, celle-ci se poursuivant tout l'hiver.

Dans une yeuseraie non brûlée de la même région, des piégeages effectués pendant des périodes identiques, montrent là aussi, un repos estival manifeste (Fig. 2 B) qui intervient après une activité sexuelle importante au printemps, et une activité sexuelle d'hiver qui serait peut-être cependant moins accentuée que dans la subéraie. Les jeunes ne sont apparus abondamment dans les piégeages de février qu'une seule fois, en 1982. La reproduction

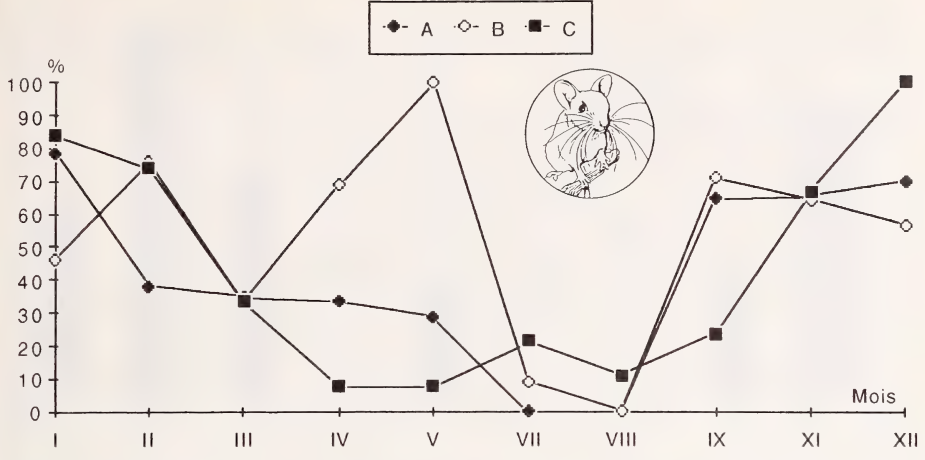


Fig. 2. Pourcentages mensuels des adultes en activité sexuelle chez *Apodemus sylvaticus* en milieu méditerranéen continental (Pyrénées-Orientales), durant six cycles annuels. A: maquis arboré à *Quercus suber* (n = 462), B: maquis arboré à *Q. ilex* (n = 284), C: (d'apres SANS-COMA et GOSALBEZ, 1976), principalement chênaie à *Q. ilex* (Montseny, Catalogne espagnole)

hivernale n'est donc peut-être pas régulière, mais le repos estival est ici aussi particulièrement net.

Tout récemment, le piégeage sur un quadrat de 9 ha mis en place en mars 1991, en milieu méditerranéen (maquis bas à chênes kermès), confirme nos résultats (Fig. 3).

Corse

Des piégeages au niveau de la mer ont été réalisés, d'une part, dans la vallée du Fango, au nord-ouest de l'île et d'autre part dans la réserve naturelle de Scandola (côte nord-occidentale), sur un quadrat prolongé par 3 lignes de pièges. L'ensemble possède une

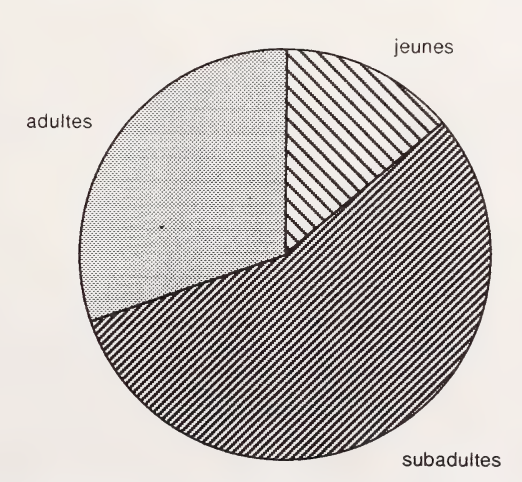


Fig. 3. Structure d'une population de 214 *Apodemus sylvaticus* (110 mâles et 104 femelles) suivie du 15 au 18 mai 1991 (plan-quadrat, biome méditerranéen, Pyrénées-Orientales). Alors que 100 % de la population est au repos sexuel total, la présence de jeunes (14,01 %) et de subadultes (55,5 %) démontre clairement une reproduction antérieure hivernale

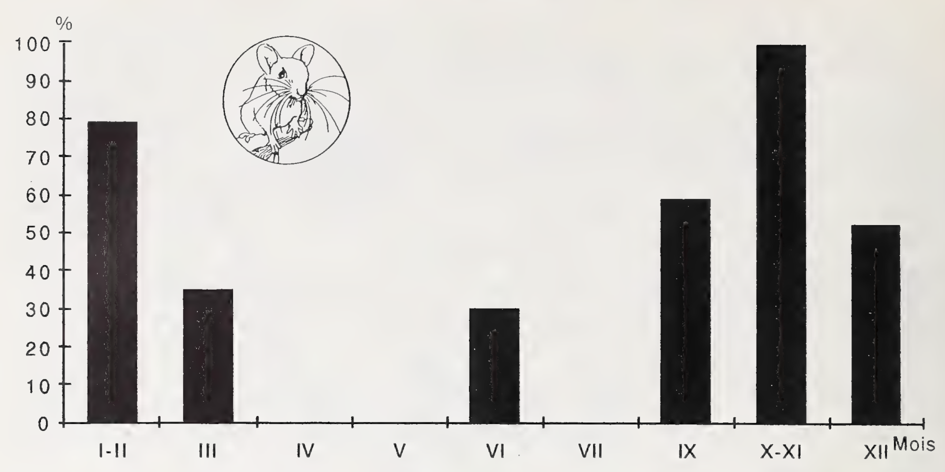


Fig. 4. Pourcentages mensuels durant 3 cycles annuels, des adultes (n = 223) en activité sexuelle chez *Apodemus sylvaticus* en milieu méditerranéen insulaire (divers stades de maquis et ripisylve); Réserve naturelle de Scandola et vallée du Fango, nord-ouest de la Corse

surface de 3,76 ha et présente 5 faciès principaux: friches, divers stades de maquis et ripisylve dense en bordure de ruisseau à sec. Au cours des six sessions de piégeage (capture-marquage-lâcher-recapture/4 nuits consécutives) réalisées sur ce quadrat, 138 rats noirs (*Rattus rattus*), 338 souris (*Mus domesticus*) ont été suivis parallèlement à 175 *A. sylvaticus*. La reproduction d'hiver chez le mulot est là aussi manifeste car au début du printemps, les populations sont à leur maximum de densité et comprennent un grand nombre de jeunes individus. Le poids moyen des animaux capturés est de 18,3 g. en mars (35 individus) alors que, en octobre-novembre, 18 individus pesaient en moyenne 27,05 grammes. En octobre–novembre, les adultes sont tous en activité sexuelle; en avril–mai et en juillet, ils sont tous au repos sexuel (Fig. 4).

Afrique du Nord

Nos données personnelles concernent le Maroc. Elles sont peu nombreuses et fragmentaires. Nous avons simplement pu établir l'existence, en montagne, de deux saisons de reproduction, l'une au printemps, l'autre en automne (Moyen, Atlas et Rif) (Saint Girons 1972). Des données bibliographiques viennent compléter et étayer ces observations pour l'Algérie (Kowalski 1985), la Tunisie (Bernard 1969) et le Maroc (Harich et Benazzou 1990).

Discussion

En Algérie, Kowalski (1985) a étudié une population de *A. sylvaticus* au voisinage d'Oran, sur les pentes du Mourdjajo, à une altitude voisine de 300 m, exposées au nord et couvertes de forêts de chênes-lièges. Des individus ont également été capturés en montagne à 1800–2000 m, dans une forêt de cèdres des Aurès, ainsi que dans des prairies du Djurjura, vers 1730 m. Les résultats d'Oranie concordent parfaitement avec ce que nous avons pu mettre en évidence sur le littoral corse et dans les collines de Catalogne. C'est ainsi que la densité atteint son minimum en automne dans le Tell algérien comme en Corse. Elle commence à augmenter au début de l'année pour atteindre un maximum en avril, comme à Scandola. Les mâles sont actifs de septembre à février et le repos est total de mai à juillet. On trouve des femelles en gestation d'octobre à décembre et en lactation de décembre à février. On peut donc en déduire l'existence d'une période de repos estivale suivie d'une

activité hivernale, comme ce qui a été observé en Catalogne et dans la plaine côtière du Maroc (Harich et Benazzou 1990). En revanche, en altitude, la reproduction se poursuit en été comme nous l'avions noté au Maroc.

En Tunisie, bernard (1969) signale qu'il n'a capturé de femelles en gestation qu'entre septembre et février. Les mâles n'ont de testicules développés qu'entre août et mars. Cet auteur a travaillé dans les plaines côtières du nord du pays, dans la région de Tunis.

Dans la partie occidentale du bassin méditerranéen, Sans-Coma et Gosalbez (1976) ont étudié la reproduction du mulot dans le nord-est de l'Espagne, région du Montseny d'une part, chaîne pyrénéenne d'autre part. Dans les collines du Montseny les jeunes sont les plus fréquents dans les piégeages en décembre, janvier et février, attestant d'une période de reproduction en automne et en hiver et d'un ralentissement estival très accentué. La figure 2 C, basée sur les données de ces auteurs, indique les pourcentages mensuels des adultes des deux sexes en activité sexuelle. Le cycle sexuel est totalement différent en altitude ainsi que l'indique la figure 5 établie d'après les mêmes principes. Les jeunes apparaissent dans les piégeages en juillet-août et la répartition saisonnière des adultes en activité sexuelle montre l'existence d'une saison de reproduction très tranchées d'avil à septembre.

D'autres observations sont en revanche tout à fait contradictoires. Jamon (1986) a étudié, en Camargue, des populations de mulots pendant deux années consécutives et constaté une activité sexuelle débutant en mars et avril et se terminant en août. La densité des mulots est maximale en automne et minimale au printemps, excluant donc la possibilité de toute reproduction hivernale. Ces observations ont été faites dans une zone herbeuse parsemée de buissons d'une part, une sansouïre partiellement inondée l'hiver d'autre part. La saison de reproduction ne diffère pratiquement pas entre ces deux zones. Elle correspond tout à fait à celles observées en Bretagne et dans la Région Parisienne ainsi que, en général, dans toute l'aire européenne de répartition du mulot au nord de la région méditerranéenne (Baker 1930; Raynaud 1950a,b; Bergstedt 1965; Birkan 1968).

Nous avons recherché si des modifications du cycle sexuel propres à la région méditerranéenne se manifestaient également chez d'autres espèces de muridés. En particulier chez la souris sauvage, *Mus spretus* et la souris domestique *M. domesticus,* qui vivent dans les mêmes zones que le mulot en utilisant des biotopes plus ouverts, ainsi que chez le rat noir, *Rattus rattus,* qui vit à l'état sauvage dans les îles méditerranéennes.

Peu de travaux ont été consacrés à ce genre de recherche. Vargas et al. (1986), Antunez et al. (1990) montrent que la reproduction de *Mus spretus* commence au début de mars et se termine à la fin de novembre dans la région de Malaga (Sud de l'Espagne), avec deux maxima d'intensité, l'un en avril-mai, l'autre en août–septembre. Il n'y a pas d'activité sexuelle en hiver. Le schéma de la reproduction est donc comparable à celui présenté par *A. sylvaticus* mais en zone médio-européenne et non en zone méditerranéenne. Chez la même espèce, Duran et al. (1987) notent que si la nourriture est abondante, l'activité sexuelle est continue. Dans le cas contraire, 3 maxima annuels (février–mars, juin–juillet et octobre–novembre) alternent avec 3 minima.

Chez le rat noir, non anthropique, de l'île de Port-Cros (côte varoise), l'activité sexuelle se poursuit pendant la plus grande partie de l'année et ne cesse totalement qu'en plein été (Cheylan et Granjon 1985). Au sud de l'Espagne, Zamorano et al. (1987) montrent que l'activité sexuelle dure de février à octobre et que certains mâles au moins peuvent se reproduire en automne.

Nous avons étudié dans des conditions rigoureusement identiques les périodes de reproduction du mulot, de la souris (*M. domesticus* car *M. spretus* est absente de l'île) et du rat noir dans la nature en Corse. Si *A. sylvaticus* se reproduit l'hiver et se trouve au repos l'été (Fig. 4), c'est exactement le contraire chez *R. rattus* et *M. domesticus.* La densité des trois muridés a été estimée par l'indice de Lincoln à partir des effectifs capturés (Granjon et Cheylan 1988). Le cycle de la souris et celui du rat sont corrélés positivement ($r = 0{,}787$

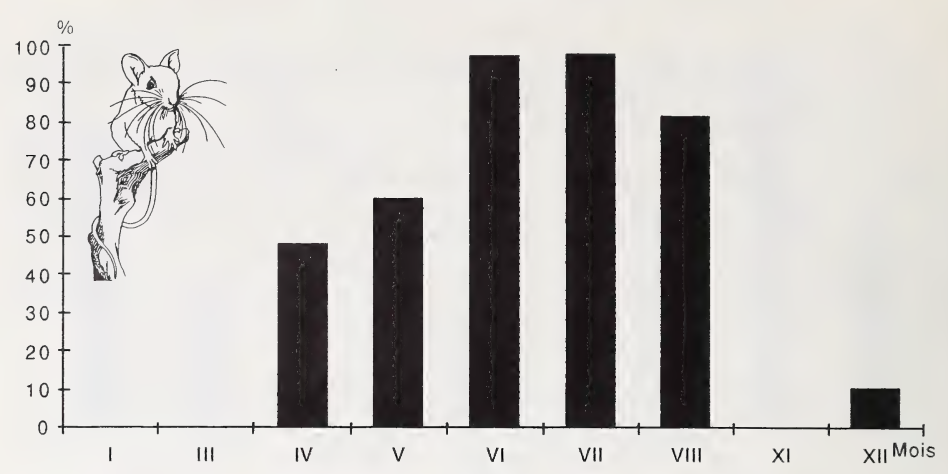


Fig. 5. Pourcentages mensuels des adultes en activité sexuelle chez *Apodemus sylvaticus* en zone pyrénéenne d'altitude (d'après SANS-COMA et GOSALBEZ 1976)

0,10 < p < 0,05) alors que celui du mulot est corrélé négativement avec celui des deux autres espèces (avec la souris r = −0,236; avec le Rat r = −0,309). Le décalage temporel du cycle démographique du mulot par rapport a celui des deux autres muridés est du même type que celui rencontré en Italie entre *M. domesticus* et *A. sylvaticus* par BOITANI et al. (1985) dans un milieu littoral où vit également *R. rattus*. Pour ces auteurs ce mécanisme aurait pour but de réduire la compétition entre les deux espèces et aurait donc un caractère adaptatif. En Corse, GRANJON et CHEYLAN (1988), évoquent le même phénomène pour permettre la coexistence équilibrée des trois espèces.

Le déterminisme du cycle sexuel du mulot est donc variable suivant la latitude et l'altitude mais avec des exceptions (Camargue). Pour expliquer la périodicité des cycles sexuels des Vertébrés, de nombreux auteurs ont mis l'accent sur la coïncidence entre l'activation des gonades et l'augmentation de la durée de l'éclairement qui débute fin décembre-début janvier. Si l'on admet cette hypothèse, on ne comprend pas pourquoi le début de l'activité sexuelle se place en mars chez les mulots de Camargue et en septembre–octobre en Catalogne. De même, pourquoi les mulots de la région de Barcelone seraient-ils en activité sexuelle en novembre alors que ceux des Pyrénées, quelques dizaines de kilomètres au nord, sont au repos sexuel et ne commenceront à devenir actifs qu'en avril?

Une autre hypothèse a été émise par RAYNAUD (1951a, b) qui a obtenu l'activation sexuelle chez les mulots adultes en hiver en fournissant une nourriture abondante à des animaux maintenus en captivité à l'extérieur. DELOST (1960), reprenant les données publiées, montre que l'alimentation est sans doute le facteur essentiel quant à la saison de reproduction, sans toutefois déterminer si cette influence est qualitative ou quantitative.

Cette hypothèse est confortée par nos observations, particulièrement celles relatives aux populations montagnardes de zones par définition plus humides, qui présentent un cycle sexuel comparable à celui des mulots de zone médio-européenne (Maroc, Pyrénées-Orientales). Des exceptions comme celles de la Camargue peuvent s'expliquer par l'existence dans ce cas d'une nappe phréatique peu profonde et des inondations régulières en hiver, ce qui se répercute bien entendu sur la végétation quantitativement et qualitativement.

Remarquons que ce qui apparaît le plus régulièrement dans le cycle sexuel des animaux en zones chaudes et sèches, c'est l'arrêt au cours de l'été. La reproduction hivernale est moins régulière. Elle fait parfois défaut, comme nous l'avons vu dans les chênaies des

collines méditerranéennes et, inversement, elle peut se manifester en Europe moyenne (Saint Girons 1967), voire continentale (Le Louarn et Saint Girons 1977) ou même septentrionale (Formozov 1962).

L'influence de la qualité et/ou de la quantité de nourriture disponible sur le cycle sexuel des rongeurs semble maintenant admise par la plupart des mammalogistes (Le Louarn et Schmitt 1972; Flowerdew 1973; Jamon 1986). Le mulot est un bon exemple de cette adaptation. La diminution de la nourriture disponible l'été en région méditerranéenne sèche et chaude coïncide avec un repos sexuel complet. L'activité sexuelle, au contraire se manifeste après les pluies d'automne déterminant une réponse de la végétation et se poursuit généralement tout l'hiver.

Les peuplements de micromammifères présents sur les îles du bassin méditerranéen nord occidental se singularisent par un ensemble de modifications ou *syndrome insulaire* (Mac-Arthur et Wilson 1967; Blondel 1979, 1986) qui les distinguent de leurs homologues continentaux: appauvrissement spécifique, relâchement subséquent des pressions de prédation et de compétition, phénomènes de compensation des densités, élargissement de la niche écologique, modifications génotypiques et phénotypiques (Libois et Fons 1990; Fons et Mas-Coma 1991). Si ces modifications de traits biologiques, démographiques et sociaux de caractère adaptatif engendrent un mécanisme de coexistence spécifique dans une guilde de muridés insulaire (Grandjon et Cheylan 1988), on ne peut attribuer au syndrome d'insularité l'inversion du cycle d'activité du mulot en Corse par rapport à la partie moyenne de l'aire de répartition européenne de l'espèce . Le même phénomène se produit dans les régions côtières du nord de la Méditerranée (Roussillon, Catalogne) comme du sud (Maroc, Algérie, Tunisie). En Corse où le mulot se trouve en forte concurrence avec le rat et la souris, il garde cependant l'*adaptation méditerranéenne* de son cycle sexuel.

Les capacités adaptatives de *A. sylvaticus* s'exercent de façon très nette en ce qui concerne le déterminisme et la durée du cycle sexuel. En région méditerranéenne, le mulot a développé une *«réponse stratégique»* de la reproduction remarquablement adaptée au milieu alors que d'autres muridés, rat et souris, conservent des cycles pratiqués sur l'ensemble de leur aire de répartition.

Remerciements

Ce travail doit beaucoup à C. H. Bianconi pour son aide constante et déterminante lors de missions scientifiques de terrain en Corse. J. Cl. Auffray, G. Cheylan, J. P. Clara, H. Croset, H. Gaubert, L. Granjon, M. Navajas, O. Pouliquen ont participé aux suivis du plan-quadrat dans la Réserve naturelle de Scandola. M. Salotti nous a fourni un matériel précieux de différentes localités de l'île. Depuis de nombreuses années nous bénéficions de l'aide de M. Leenhardt, Directeur de Parc Naturel Régional de la Corse ainsi que du personnel et de J. Trave, gestionnaire de la Réserve Naturelle de la Massane. Qu'ils soient tous assurés de notre reconnaissance.

Zusammenfassung

Zum Reproduktionszyklus der Waldmaus, Apodemus sylvaticus (L., 1758) (Muridae) im Mittelmeerraum

Zur Untersuchung des Reproduktionszyklus wurden Daten von 1301 Individuen der Waldmaus *Apodemus sylvaticus* aus dem Gebiet des Mittelmeeres gesammelt und ausgewertet. Diese wurden mit entsprechenden Angaben für Populationen aus der Bretagne und Nordafrika verglichen. Besondere Beachtung fand der Reproduktionszyklus korsischer Waldmäuse. In Bezug auf Beginn und Dauer der aktiven Reproduktionsperiode zeigt die Waldmaus deutliche Anpassungen an regionale Bedingungen. In Mitteleuropa und in höheren Lagen des Mittelmeerraums ist die Waldmaus von Frühlingsbeginn bis Herbstende sexuell aktiv. Im Winter hat sie eine sexuelle Ruhephase. Im Gegensatz dazu findet die sexuelle Aktivität in Küstengebieten und Insellagen des Mittelmeeres im Winter und im Frühling statt, die Ruhephase ist im Sommer.

Zwischen dieser Anpassung und dem Inselphänomen scheint es keinerlei Verbindung zu geben. Andere Vertreter der Muridae (*Rattus rattus, Mus musculus* und *Mus spretus*) zeigen keine vergleichbare Anpassung im Reproduktionszyklus. Sie folgen im gesamten westlichen Teil ihres Verbreitungsgebietes demselben Rhythmus. Im Mittelmeerraum zeigt *Apodemus sylvaticus* demnach eine Anpassung der Reproduktionsphase an das Vorhandensein von Nahrungsressourcen, die ihrerseits durch klimatische Faktoren festgelegt sind.

Bibliographie

Antunez, A.; Vargas, J. J.; Sans-Coma, V.; Palomo, L. J. (1990): Quelques aspects du cycle biologique de *Mus spretus* Lataste, 1883, au sud de la Péninsule ibérique. Vie Milieu **40**, 196–200.

Baker, J. R. (1930): The breeding season in British wild mice. Proc. Zool. Soc. **8**, 113–126.

Bergstedt, B. (1965): Distribution, reproduction, growth and dynamics of the rodent species *Clethrionomys glareolus* (Schreber), *Apodemus flavicollis* (Melchior) and *Apodemus sylvaticus* (L) in Southern Sweden. Oïkos **16**, 132–160.

Bernard, J. (1969): Les Mammifères de Tunisie et des régions voisines. Bull. Fac. Agronomie **24–25**, 41–172.

Birkan, M. (1968): Répartition écologique et dynamique des populations d'*Apodemus sylvaticus* et *Clethrionomys glareolus* en pinède de Rambouillet. Terre Vie **3**, 231–273.

Blondel, J. (1979): Biogéographie et Ecologie. Paris: Masson Ed.

— (1986): Biogéographie évolutive. Paris: Masson Ed.

Boitani, L.; Loy, A.; Molinari, P. (1985): Temporal and spatial displacement of two sympatric rodents (*Apodemus sylvaticus* and *Mus musculus*) in a Mediterranean coastal habitat. Oïkos **45**, 246–252.

Cheylan, G.; Granjon, L. (1985): Ecologie d'une population de rats noirs *Rattus rattus* à Port-Cros (Var). Méthodologie et premiers résultats obtenus sur quadrat. Sc. Rep. Port-Cros Natl. Park Fr. **11**, 119–130.

Duran, A. C.; Camprodon, F. J.; Cardo, M.; Sans-Coma, V. (1987): La reproduccion de *Mus spretus* Lataste, 1883 en el N-NE de la Peninsula iberica. *In*: Mamiferos y Helmintos. Barcelona: Ketres Ed. pp. 111–120.

Delost, P. (1960): Nutrition et cycles endocriniens chez les Mammifères sauvages non hibernants. Ann. Nutrition Alimentaire **14**, 53–104.

Flowerdew, J. R. (1973): The effect of natural and artificial changes in food supply on breeding in woodland mice and voles. J. Reprod. Fert., Suppl. **19**, 259–269.

Fons, R.; Grabulosa, I.; Saint Girons, M. C.; Galan-Puchades, M. T.; Feliu, C. (1988): Incendie et cicatrisation des écosystèmes méditerranéens. Dynamique du repeuplement en micromammifères. Vie Milieu **38**, 259–280.

Fons, R.; Mas-Coma, S. (1991): Système «*hôte-parasite*» et «*syndrome insulaire*»: Les micromammifères et leurs helminthes parasites dans les îles du bassin méditerranéen nord-occidental. Congr. Intern. Asoc. Sudoccidental Europeas de Parasitologia-ICASEP I, Valencia (sous presse).

Formozov, A. N. (1962): A study of mammalian ecology under the conditions of snowy and cold winters of Northern Eurasia. Symp. Ther. Brno **1960**, 102–111 (en russe, rés.anglais).

Grandjon, L.; Cheylan, G. (1988): Mécanismes de coexistence dans une guilde de muridés insulaires (*Rattus rattus* L., *Apodemus sylvaticus* L. et *Mus musculus domesticus* Rutty) en Corse: Conséquences évolutives. Z. Säugetierkunde **53**, 301–316.

Harich, N.; Benazzou, T. (1990): Contribution à l'étude de la biologie du mulot (*Apodemus sylvaticus*) (Rongeurs, Muridés) de la plaine côtière du Maroc. Mammalia **54**, 47–59.

Herrenschmidt, V. (1978): Contribution à la connaissance des micromammifères de la Réserve Naturelle de la Massane. Tr.n°20 offset, Labo. Arago.

Jamon, M. (1986): The dynamics of wood mouse (*Apodemus sylvaticus*) populations in the Camargue. J. Zool. London A. **208**, 569–582.

Kowalski, K. (1985): Annual cycle of reproduction in *Apodemus sylvaticus* in Algeria. Acta Zool. Fennica **173**, 85–86.

Le Louarn, H.; Saint Girons, M. C. (1977): Les rongeurs de France. Ann. Zoologie-Ecologie animale I.N.R.A., n° hors série.

Le Louarn, H.; Schmitt, A. (1972): Relations observées entre la production en faînes et la dynamique de population du mulot, *Apodemus sylvaticus* L., en forêt de Fontainebleau. Ann. Sc. Forest **30**, 205–214.

Libois, R.; Fons, R. (1990): Le mulot des îles d'Hyères: un cas de gigantisme insulaire. Vie Milieu **40**, 217–222.

Mac-Arthur, R.; Wilson, E. (1967): The theory of island biogeography. Princeton: Princeton University Press.

Quezel, P. (1974): Les forêts du pourtour méditerranéen. U.N.E.S.C.O. Programme Homme et Biosphère, Comm. Nat. fr. MAB.

RAYNAUD, A. (1950a): Etat de développement de l'appareil génital des mulots (*Apodemus sylvaticus*) au cours des différentes saisons de l'année C.r. Soc. Biol. **144**, 938–940.
— (1950b): Variations saisonnières des organes génitaux des mulots, *Apodemus sylvaticus,* L. de sexe mâle. Données pondérales et histologiques. C. R. Soc. Biol. **144**, 941–945.
— (1951a): Recherches sur les variations saisonnières de l'activité génitale des mulots (*A. sylvaticus* L.) du département du Tarn. Bull. Soc. Hist. nat. Toulouse **86**, 133–150.
— (1951b): Spermatogenèse active en hiver chez les mulots (*Apodemus sylvaticus* L.) élevés dans une cage placée à l'extérieur, dans un jardin. C. R. Soc. Biol. **145**, 1063–1069.
SAINT GIRONS, M. C. (1955): Notes sur l'écologie des petits mammifères du bocage atlantique. Terre Vie **1**, 4–41.
— (1957): Les mammifères des Pyrénées-Orientales I – Observations sur quelques mammifères recueillis dans la région de Banyuls et plus particulièrement le mulot. Vie Milieu **8**, 287–296.
— (1972): Le genre *Apodemus* Kaup, au Maroc. Z. Säugerierkunde **37**, 362–371.
SAINT GIRONS, M. C.; WODZICKI, K. (1985): Les rongeurs et la culture du maïs dans un bocage de l'ouest de la France. Bull. Soc. Sci. nat. Ouest de la France; N.S. **7**, 1–10.
SANS-COMA, V.; GOSALBEZ, J. (1976): Sobre la reproduccion de *Apodemus sylvaticus* L., 1758 en el nordeste iberico. Miscelanea Zoologica **3**, 227–233.
TORREGROSA ORTS, M.; FELIU, C.; FONS, R. (1987): Contribution à la connaissance des helminthes parasites de micromammifères I. Parasites de *A. sylvaticus* L. 1758 (Rodentia-Muridae). Trav.n°22 Rés. nat. Massane, offset Labo. Arago.
VARGAS, J. M.; PALOMO, L. J.; ESPANA, M.; DURAN, A. C.; SANS-COMA, V. (1986): Über die Geschlechtstätigkeit der Weibchen und die Populationsstruktur von *Mus spretus* Lataste, 1883 in Südspanien. Z. angewandte Zool. **73**, 219–229.
ZAMORANO, E.; VARGAS, J. M.; PALOMO, J. L. (1987): Estrategias de la reproduccion de *Rattus rattus* L. 1758 en el sur de la Peninsula Iberica. In: Mamiferos y Helmintos. Barcelona: Ketres Ed. pp. 99–110.

Adresse des auteurs: Dr. ROGER FONS, Laboratoire Arago, Université Pierre et Marie Curie, Unité Associée au CNRS n°117, F-66650 Banyuls-sur-Mer et Dr. MARIE CHARLOTTE SAINT GIRONS, Laboratoire d'Evolution des Etres Organisés, 105 bd. Raspail, F-75005 Paris, France

Z. Säugetierkunde 58 (1993) 48–53

ISSN 0044-3468

Size variation in *Rhabdomys pumilio:* A case of character release?

By Y. Yom-Tov

J. R. Ellerman Museum, Department of Zoology, University of Stellenbosch, Stellenbosch, South Africa and Department of Zoology, Tel Aviv University, Tel Aviv, Israel

Receipt of Ms. 4. 2. 1992
Acceptance of Ms. 24. 2. 1992

Abstract

Studied size variation in the striped mouse *Rhabdomys pumilio,* a diurnal herbivorous murid, across southern Africa using the greatest length of the skull (GTL) as a measure of body size. There was a positive correlation between GTL and the mean minimum temperature of the coldest month (July), contrary to Bergmann's rule, but there was no significant correlation between GTL and either mean maximal annual temperature, mean maximal temperature of the hottest month (January), altitude or annual rainfall. There were differences in size between samples of different biotic regions: Animals from the south west Cape were largest, followed by those from the Namib desert, forest, south west arid zone, and the savanna, respectively.

Animals from the zone of sympatry with *Lemniscomys griselda,* a larger herbivorous diurnal murid, were significantly smaller than those from allopatric zones. It is suggested that character release is a primary factor in determining body size of *R. pumilio* in southern Africa.

Introduction

The striped mouse *Rhabdomys pumilio* is a small (30–35 g), diurnal murid which is widely distributed in eastern and southern Africa. It occupies a wide range of habitats, all of which have some cover of grass, at latitudes of up to 1800 m above sea level in Zimbabwe (Smithers 1983), but avoids tropical woodland savannas and parts of the central Karoo where there is no grass (De Graaf 1981). Throughout its large distribution area it varies greatly in colour and size. This situation led to conflicting conclusions regarding its taxonomic state: Roberts (1951) recognized 20 subspecies for the southern Africa subregion alone while others stated that their status is doubtful (Meester et al. 1986). Coetzee (1970) came to the conclusion that it is impossible to recognize subspecies and that at the most there is a pale coloured western and a dark coloured eastern form. Some morphological trends were determined: Specimens from the Cape Province are larger than those from Zimbabwe (Roberts 1951) and specimens from high altitudes in the Drakensberg Mountains have shorter tails than those from lower altitudes (Rowe-Rowe and Meester 1985). The genus is monospecific.

Size variation in mammals and other animals has been correlated with several abiotic and biotic factors. Among the abiotic factors, probably the most commonly mentioned in the literature are those which relate body size or the relative size of body extremities (legs, tails and ears) to ambient temperature. According to the rule of Bergmann (1847), races of warm blooded animals which live in warm climates have smaller body size than their relatives which live in cold climates (Mayr 1970). Body size might be correlated with food availability, as have been shown by Yom-Tov and Nix (1986). It might also be influenced by interspecific competition, either through character displacement or character release (Brown and Wilson 1956; Lincoln et al. 1982).

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5801-0048 $ 02.50/0

The aim of this paper is to discern which factor or factors are likely to determine the variation which exists in body size between the southern African populations of *R. pumilio*.

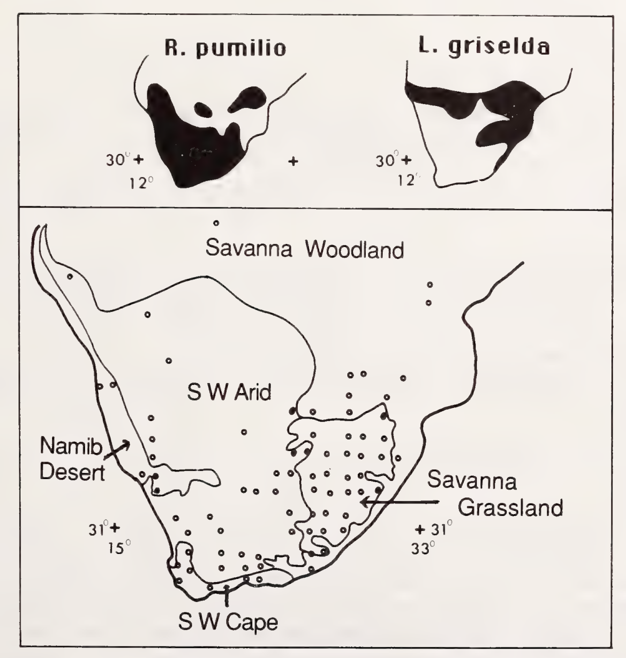
Material and methods

Skulls of adults which have been collected in South Africa, Namibia, Botswana, Zimbabwe and Lesotho, were measured in the following museums in South Africa: The John Ellerman Museum, University of Stellenbosch; South African Museum, Capetown; The Kaffarian Museum, King William's Town; The National Museum, Bloemfontein; and the Transvaal Museum, Pretoria. The geographical range of the specimens in this study ranged from 18° S in Namibia and Zimbabwe to 34° 29′ S in the Cape Province of South Africa and from 13° E in Namibia to 32° 40′ E in Zimbabwe.

In this study the skull length was used as a comparative measure of body size. The greatest length of the skull (GTL) in its midline from the front of the upper incisors to the posterior margins of the skull was measured with digital calipers to accuracy of 0.01 mm. Only skulls with complete fusion of the bones and fully grown teeth were measured. Since no sexual dimorphism in size was detected in this species (Smithers 1983), the data for males and females were pooled.

The desired sample size for this study was to obtain 20 specimens from each degree square of southern Africa, south of 18° S. There are about 280 such squares, but specimens were available for only 77 (Figure). The best represented areas were those south and east of the line stretching from the south west Cape province (30° S 17° E) to north east Natal (20° S 30° E) which contains about 120 squares of which 63 contained samples. However, there were very large areas, especially in the Kalahari Desert, from which no specimens were available. For some squares which vary greatly in latitude more than one sample was measured, so that altogether there are 92 samples from 85 degree squares in this study, totaling 1260 specimens.

Climatological data were taken from the nearest weather station to the locality of each sample, using long term data published by the South African Weather Bureau (Climate of South Africa 1986). Some of the specimens, mainly from areas which are densely populated by humans, came from localities which were within a range of a few kms from a weather station, but many others,



Biotic zones of southern Africa (after Davis 1962) and locations of the samples measured in this study. The upper maps are the distribution areas of *Rhabdomys pumilio* and *Lemniscomys griselda* (after Smithers 1983). Forest areas are not marked on the map, as they are too small. Circles indicate locations of the 77 samples examined in this study

particularly from remote localities in Namibia and Botswana, were collected many kms from the nearest weather station. However, since these areas generally consist of wide plains, it is likely that the data from the nearest weather station does not differ much from the actual local weather.

The means of GTL of each sample were regressed against the following climatological data: mean annual rainfall, mean maximal annual temperature, mean maximal temperature of the warmest month (January) and mean minimal temperature of the coldest month (July).

In order to examine the possibility that altitude affects skull size, one degree square (31° S 27° E) which varies greatly in altitude (1000–2100 m above sea level), was sub-divided into 16 quarter degrees squares. For 10 of these squares there were samples of skulls (4–20 in each, mean = 12.7), for each of which the mean of their GTL was calculated and regressed against the altitude from which the skulls were collected.

Southern Africa can be geographically subdivided into different biotic zones, differing from each other climatologically and vegetationally. The classification used in this study is that used by Meester (1965, after Keay 1959 and Davis 1962).

In order to test the possibility that body size of *Rhabdomys* is different in zones of sympatry and allopatry with *Lemniscomys,* mean GTL was calculated for these zones using the distribution maps for these species in Smithers (1983).

Results

There was no significant correlation between GTL and either annual rainfall, altitude, mean maximal temperature in January or mean maximal annual temperature, but contrary to Bergmann's rule, there was a positive significant correlation between GTL and mean minimal temperature of the coldest month (July, $r = 0.6679$; $p = 0.009$). Mean GTL is 29.88 and 28.42 mm in areas where mean minimal July temperatures are −3 °C and 10 °C, respectively.

There were differences in skull size between samples of different biotic regions. The largest skulls belonged to animals from the south west Cape, followed by those from the Namib desert, forest, south west arid zone and the savanna (grassland and woodland), in this order (Tab. 1). There was little variation in size within each zone, the coefficient of variation ranged between 1.4–4.1 %. Animals from the south west Cape were significantly larger than those from all other zones except the forest, and those of the savanna were significantly smaller than animals from all other zones. There were also some significant differences between the other groups (Tab. 2).

Mean GTL (and standard deviation) of *Rhabdomys* in the zones of sympatry and allopatry with *Lemniscomys* are 26.0 (SD = 0.7; range 24.4–27.4; n = 26) and 27.3 mm (SD = 1.0; range 25.5–29.6; n = 58), respectively.

The correlation between GTL and mean minimal July temperature became higher ($r = 0.9267$; $p = 0.0001$) when run without the samples from locations where *Rhabdomys* is sympatric with *Lemniscomys* (i.e. only on allopatric samples). This was due to the fact that GTL of samples from areas of sympatry was smaller and came from relatively warmer (northern) areas in southern Africa. However, there was no significant correlation between any of the examined temperature parameters and GTL of the samples taken from areas of sympatry only.

Discussion

Bergmann's rule predicts that warm blooded animals which live in cold regions are larger than those of the same species which live in warm areas, i.e. a negative correlation is predicted between body size and ambient temperature. GTL of the striped mouse is not correlated with mean annual maximal temperature or mean maximal temperature of the warmest month, and, contrary to the predication of Bergmann's rule, it is positively correlated with mean minimal temperature in July.

Yom-Tov and Nix (1986) have shown that biomass productivity is correlated with body size in three species of Australian mammals. Different biotic zones often have

Table 1. **Mean and standard deviation (SD) and the coefficient of variation (CV, %) of GTL of *Rhabdomys pumilio* in various biotic zones of southern Africa**

Zone	n, groups	n, specimens	Mean	SD	CV
Namib	5	76	28.0	0.4	1.4
South West Cape	7	108	28.7	0.6	2.1
Forest	4	52	27.9	1.1	4.1
South West Arid	27	380	27.2	0.7	2.5
Southern Savanna	30	472	26.2	0.7	2.8
Southern Savanna Woodland	12	172	26.1	0.6	2.4
Total	85	1260			

Table 2. **Results of T-test comparing mean GTL of the various biotic zones of southern Africa**
In each comparison the upper figure is the t value, the lower its probability. NS – Not significant

Zone	SW Cape	Forest	SW Arid	Southern Savanna	
				Grassland	Woodland
Namib	2.4 0.05	1.8 NS	3.6 0.001	8.57 0.001	7.6 0.001
SW Cape		1.36 NS	5.76 0.001	9.61 0.001	9.29 0.001
Forest			1.25 NS	3.04 0.01	3.16 0.01
NW Arid				5.56 0.001	4.45 0.001
S Savanna Grassland					0.48 NS

different productivity, to which body size might be correlated. There have been various attempts to subdivide Southern Africa into biotic zones, but Davis's (1962) classification is the most accepted today (Meester 1965; Rautenbach 1978). According to this classification there are four biotic zones in this region, two of which are subdivided into two distinct subregions (totalling six zones):

Southern savanna which encompasses the wetter eastern part of southern Africa, with more than 500 mm annual rainfall. This zone has two distinct subregions – grassland in its south and woodland in the north and the eastern coast.

South West Arid which consists of the arid western part of southern Africa, with a mean annual rainfall less than 500 mm. The Namib desert of the western coastal strip is recognized as a distinct subregion.

Forest, which consists of isolated patches of montane and subtropical evergreen forest in the savanna and west Cape regions.

South West Cape, a climatically and biotically distinct zone which corresponds to the Cape macchia.

In southern Africa, as in other dry environments, precipitation is associated with primary production. Since GTL is not correlated with rainfall, it does not appear that primary production affects size in the striped mouse.

By way of elimination, the above findings indicate that the factor which determines the significant differences in GTL is biotic rather than abiotic. Among the biotic factors, interspecific competition, particularly over food, was shown to affect size in various animals. Character displacement is a situation in which, where two species of animals

overlap geographically, the differences in size between them are accentuated in the zone of sympatry and weakened or lost in the parts of their ranges outside this zone (Brown and Wilson 1956). This phenomenon arises from competition between the two, and the removal of the larger of the two species may be followed by an increase in the variation in some phenotypic character, a situation termed character release (Lincoln et al. 1982). Recently, Alcantara (1991) has shown that there is an increase from north to south in body size of the wood mouse *Apodemus sylvaticus*, contrary to Bergmann's rule, and he raised the possibility that body size of the wood mouse is determined by competition with the yellow-necked mouse *Apodemus flavicollis*. If *R. pumilio* has a competitor, it is likely to be another diurnal rodent, similar in size, habitat and habits. There are two other genera of diurnal rodents in southern Africa, *Otomys* (seven species) and *Lemniscomys* (one species: *L. griselda*). All species of *Otomys* present in southern Africa are considerably larger than the other two diurnal genera, with body weight averaging above 100 g, while *Lemniscomys* weighs on average 58 g and *Rhabdomys* between 37–54 g (Smithers 1983). Moreover, the preferred habitats of *Otomys* are fringes of swamps, wet vleis and other wet grassy habitats while the other two diurnal rodents prefer dense grass. Both factors make *Otomys* species unlikely competitors with the other two diurnal species. However, the other two genera are very similar: both belong to the Murinae, prefer the same habitat (dense grass) and are largely granivorous (*Otomys* is largely herbivorous). The only consistent anatomical difference between *Lemniscomys* and *Rhabdomys* would seem to be that *Lemniscomys* has a much reduced fifth digit in the forefoot while *Rhabdomys* has five normal digits (Roberts 1951). *Lemniscomys* is slightly larger than *Rhabdomys* (GTL ranges between 30.5–35.5 and 26.0–30.8 mm, respectively; Roberts 1951), and it is reasonable to assume that it will be more successful when competing with the smaller *Rhabdomys* where they are sympatric.

I suggest that the relatively large GTL of the striped mouse in the south-west Cape, forest and the Namib desert relative to that in the savanna might be explained as a case of character release. The distribution areas of the two genera in southern Africa overlap to some extent: While *Rhabdomys* occurs in all six biogeographic zones of southern Africa, *Lemniscomys* occupies the southern savanna woodland, the northern part of the grassland and the northern areas of the south west arid zone (Smithers 1983), where the two species are sympatric. It is reasonable to assume that *Rhabdomys* is larger in areas where it is allopatric with *Lemniscomys* due to the absence of its larger competitor, i.e. due to character release. This situation is remarkably similar to that found recently by Alcantara (1991) for wood mice in Europe: In both studies the size of the smaller species of the two possible competitors (*Apodemus sylvaticus* in Europe, *Rhabdomys pumilio* in southern Africa) is positively correlated with ambient temperature, contrary to Bergmann's rule, and in both size increases in the zones of allopatry with the potential competitor (*A. flavicollis* in Europe, *Lemniscomys griselda* in southern Africa).

Acknowledgements

This work would not have been possible without the help given to me by many people in South Africa. I would like to express my gratitude to Prof. Jan Nel, Head of the Zoology Department of Stellenbosch University for his exceptional hospitality in Stellenbosch; Drs. Graham Avery of the National Museum, Capetown; Richard Klein of Chicago University; Lloyd Wingate of the Kaffarian Museum, King William's Town; Johan Watson of the National Museum, Bloemfontein; Naas Rautenbach, Director of the Transvaal Museum, Pretoria; Prof. John Skinner and Prof. Rudi van Aarde of the Mammal Research Institute, University of Pretoria – all provided hospitality and help in many ways. I am grateful to them all for making my stay in South Africa enjoyable and productive. Thanks are also due to Mrs. Kristie Nel, Mr. Piet Beukes, Mr. Kenneth Payne, Mrs. Richter and the late Mrs. Patsy Skinner for their hospitality. Dr. Tamar Dayan, Dr. Avraham Haim, Prof. H. Mendelssohn and Prof. J. A. J. Nel commented on the manuscript.

This study was supported by the John Ellerman Scholarship, through the University of Stellenbosch.

Zusammenfassung

Die Größenvariation der Streifenmaus Rhabdomys pumilio: ein Fall von Merkmalsfreigabe?

Die Größenvariation der Streifenmaus *Rhabdomys pumilio,* einem tagaktiven herbivoren Nager, wurde im südlichen Afrika untersucht, wobei die größte Schädellänge (GTL) als Maß für die Körpergröße verwendet wurde. Entgegen Bergmanns Regel bestand eine positive Korrelation zwischen der GTL und der mittleren Minimaltemperatur des kältesten Monates (Juli), aber es ließ sich keine signifikante Beziehung zwischen der GTL und dem Jahresmittel der Maximaltemperatur, der mittleren Maximaltemperatur des wärmsten Monates (Januar), der Meereshöhe oder dem Jahresniederschlag belegen. Zwischen Stichproben verschiedener Herkunft bestanden deutliche Unterschiede: am größten waren die Mäuse aus der südwestlichen Kap-Provinz, gefolgt von denen aus der Namibwüste, aus Waldregionen, aus der südwestlichen Trockenzone, und aus Savannen. Tiere aus Regionen sympatrischen Vorkommens, mit *Lemniscomys griselda,* einem vergleichbaren, aber etwas größeren Nager, waren signifikant kleiner als Streifenmäuse aus allopatrischen Teilarealen. Daraus wird geschlossen, daß die Körpergröße von *Rhabdomys pumilio* im südlichen Afrika primär durch Merkmalsfreigabe bestimmt wird.

Literature

South African Weather Bureau (1986): Climate of South Africa. Pretoria: Dep. Environm. Affairs.

Alcantara, M. (1991): Geographical size variation in body size of the Wood mouse *Apodemus sylvaticus* L. Mammal Rev. **21**, 143–150.

Bergmann, C. (1847): Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. Göttinger Studien **1**, 595–708.

Brown, W. L.; Wilson, E. O. (1956): Character displacement. Syst. Zool. **5**, 49–64.

Coetzee, C. G. (1970): The relative tail length of Striped mouse *Rhabdomys pumilio* Sparrman, 1784 in relation to climate. Zool. Afric. **5**, 1–6.

Davis, D. H. S. (1962): Distribution patterns of Southern African Muridae, with notes on some of their fossil antecedents. Ann. Cape Prov. Mus. **2**, 56–76.

De Graaf, G. (1981): The rodents of Southern Africa. Durban: Butterworths.

Keay, R. W. J. (1959): Vegetation map of Africa south of the Tropic of Cancer. Oxford: Oxford Univ. Press.

Lincoln, R. J.; Boxshall, G. A.; Clark, P. F. (1982): A dictionary of ecology, behaviour and systematics. Cambridge: Cambridge Univ. Press.

Mayr, E. (1970): Population, species and evolution. Cambridge, Mass.: Harvard Univ. Press.

Meester, J. (1965): The origins of the southern African mammal fauna. Zool. Afric. **1**, 87–93.

Meester, J. A. J.; Rautenbach, I. L.; Dippenaar, N. J. D.; Baker, C. M. (1986): Classification of Southern African mammals. Transvaal Mus. Monogr. **5**, 1–359.

Rautenbach, I. L. (1978): A numerical re-appraisal of the southern African biotic zones. Bull. Carnegie Mus. Nat. Hist. **6**, 175–187.

Roberts, A. (1951): The mammals of South Africa. South Africa: The Mammals of South Africa Book Fund.

Rowe-Rowe, D. T.; Meester, J. (1985): Altitudinal variation in external measurements of two small mammal species in the Natal Drakensberg. Ann. Transvaal Mus. **34**, 49–53.

Smithers, R. H. N. (1983): The mammals of the Southern African subregion. Pretoria: Univ. Pretoria.

Yom-Tov, Y.; Nix, H. (1986): Climatological correlates for body size of five species of Australian mammals. Biol. J. Linnean Soc. **29**, 245–262.

Author's address: Prof. Yoram Yom-Tov, Department of Zoology, Tel Aviv University, Tel Aviv 69978, Israel

Z. Säugetierkunde 58 (1993) 54–61

ISSN 0044-3468

Man-made and ecological habitat fragmentation: study case of the Volcano rabbit *(Romerolagus diazi)*

By A. Velázquez

Laboratorio de Biogeografía, Facultad de Ciencias, Universidad Nacional Autónoma de México, Mexico

Receipt of Ms. 6. 4. 1992
Acceptance of Ms. 29. 6. 1992

Abstract

Documented the fragmentation of the habitat of the volcano rabbit *(Romerolagus diazi).* Two different processes of fragmentation are illustrated, namely; man-made and ecological. Man-made fragmentation has occurred through splitting the original distribution range into islands by highway construction, farming, and intensive burning and grazing activities. The ecological fragmentation is due to environmental discontinuity, which is reflected in a mosaic of vegetational communities or habitats. The ecological amplitude of the habitat types has been analyzed by canonical correlation analysis. Six habitat types were distinguished. Habitat type 2, open pine woodland *(Pinus hartwegii-Festuca tolucensis)* habitat type 3 mixed alder pine forest (*Alnus firmifolia-Muhlenbergia macroura*) and habitat type 4, pine forest (*Pinus* spp. *Muhlenbergia quadridentata*) provide most of the suitable ecological conditions for the survival of the volcano rabbit. The two processes of fragmentation habitat are threatening the survival of this endangered Mexican lagomorph. These two habitat fragmentation processes are discussed in light of their role in conservation and management.

Introduction

Habitat fragmentation can be defined as the discontinuous spatial distribution of a species within its distribution range, which originally was formed as a single continuous unit (Nilsson 1978; Haila and Hanski 1984; Soule 1986). The forming process, which is named insularization (Wilcox 1980), of this segregated distribution has been mainly attributed to various types of disturbances. These disturbances can be man-made Robbins 1979; Whitcomb et al. 1981; Lynch and Whigham 1984) or ecological (disrupting of the landscape by discontinuities of the environment; Whitaker 1973; Wilcove et al. 1986). Unlike man-made habitat fragmentation, ecological habitat fragmentation has been poorly documented. The assessment of the ecological amplitude of mammalian species requires deep understanding of habitat (mainly vegetation). Documentation on habitat fragmentation is essential for management and conservation purposes, since it has been determined as one of the major causes of extinction of species (Diamond 1984; Harris 1984; Simberloff and Abele 1984). Data gathered to study the endangered Mexican volcano rabbit (*Romerolagus diazi* Ferrari-Pérez 1893) are used to document these two types of fragmentation processes. Implications of both fragmentation processes are discussed in the light of their importance to conservation and management plans.

Study area

The distribution range of the volcano rabbit *(Romerolagus diazi)* is restricted to Central Mexico, mainly to the volcanos "Pelado", "Tláloc", "Popocatépetl", and „Iztaccíhuatl" (Hoth et al. 1987). The area lies between 18° 50′–19° 25′ N, and 98° 30′–99° 16′ W. The altitude ranges from 2,600 to 5,450 m a.s.l. The topography is irregular. The dominant soil types are Andosol and Lithosol. The climate characterized by a rainy and dry season, is temperate, ranging from mild to cool, with a mean

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5801-0054 $ 02.50/0

annual temperature of 11 °C. Further, it is sub-humid, with a mean annual rainfall of approx. 1,000 mm (García 1981). According to Rzedowski (1988) there are three main vegetation communities distributed in the area: 1. alpine grassland depicted by *Festuca livida* and *Arenaria bryoides;* 2. pine forest characterized by *Pinus hartwegii* and *Pinus montezumae;* and 3. fir forest dominaed by *Abies religiosa.* A number of mammals present in the area (e.g., the gopher *Pappogeomys merriami;* the volcano rabbit *Romerolagus diazi*) are considered to be endemic species and endangered (Ceballos and Galindo 1984). The area contains a rather peculiar plant and animal assemblage both from Nearctic as well as from Neotropical origin (see Velázquez 1992 for description of the study area).

Material and methods

Man-made habitat fragmentation is illustrated by monitoring the changes observed in the distribution area of the volcano rabbit. This monitoring has been based on publications which document the distribution of the volcano rabbit (De Poorter and Van der Loo 1979; Hall 1981; Granados 1981; López-Forment and Cervantes 1981; Bell et al. 1985; Hoth et al. 1987). Recently, Velázquez et al. (1991) mapped the present distribution of this species. All authors mentioned above, attribute habitat disruption to human activities. A map showing the oldest and the most recent distribution of the rabbit was prepared in order to show the man-made habitat fragmentation.

Ecological fragmentation has been based on the study of the vegetation communities. Data from a vegetation survey carried out within the core distribution areas of the volcano rabbit were used to define the habitat types (Velázquez et al. 1992). The vegetation was sampled according to the school of Braun-Blanquet (1951). In every relevé the following data were gathered: percentage cover per species, percentage cover per vegetation-layer, percentage of rock-outcrops, percentage of bare ground, altitude, and abundance of rabbits based upon pellet-counts. The vegetation communities (resembling habitat types) were defined by performing two-way species indicator classification analysis (TWINSPAN; Hill 1979; Hill and Gauch 1980). A total of 108 sampling units was used to quantify and to relativize the abundance of the rabbit. The relative abundance was estimated for every habitat type by pellet-counts (Osterveld 1983; Gibb 1970; Krebs et al. 1986). Since the volcano rabbit defecates in defined places forming latrines (Cervantes and Martines 1992), latrine-counts were made rather than individual pellet-counts. Canonical Correspondence Analysis (CCA) was performed in order to elucidate the environmental variables that govern the major distribution of the habitat types (Ter Braak 1986, 1987), and therefore the distribution of the rabbit. The Monte Carlo Permutation Test was used to measure the significance of the "eigenvalue" of the first axes, and the Student-T Test was used as an exploratory approach to measure the statistical contribution of the environmental variables (Ter Braak 1988). The results obtained by CCA are presented in a biplot ordination diagram. This diagram shows the variables that explain most of the variation along the first two ordination axes. Furthermore, it shows the ecological amplitude of the most important habitat for the rabbit. The discussion over the ecological fragmentation of the volcano rabbit populations is based upon this ordination diagram. A level of $P < 0.05$ was considered as significant throughout the analysis.

Results

The fragmentation of the habitat caused by man is illustraed by comparing the most outstanding changes observed in the distribution range of the volcano rabbit (Tab. 1). De Poorter and Van der Loo (1979) and Hall (1981) reported a distribution range of approx. 1,500 km^2, forming one single unit. Other sources of information (Granados 1981; López-Forment and Cervantes 1981) stated that the distribution range split into three main areas, namely, Volcano "Nevado de Toluca", "Sierra Ajusco and Chichinautzin", and "Sierra Nevada". The fragmentation into these three areas was attributed mainly to deforestation and agriculture encroachment. Bell et al. (1985) and Hoth et al. (1987) documented the shrinking process of the distribution range to 280 km^2. Bell et al. (1985) and Hoth et al. (1987) restricted the distribution of the volcano rabbit to "Sierra Nevada" and "Sierra Ajusco and Chichinautzin". Furthermore, within these two sierras the species was found only in four volcanic formations; "Iztaccíhuatl", "Popocatépetl", "Tláloc", and "Pelado". According to Hoth et al. (1987) the drastic fragmentation of the habitat was caused by deforestation, agriculture encroachment, highway construction, and bunchgrass disturbances (e.g., grazing, burning). The detailed distribution map of the species given by Velázquez et al. (1991) shows the present distribution range, which is divided in 16 units.

Table 1. **Shrinking and fragmentation processes of the habitat of the Volcano rabbit *(Romerolagus diazi)***

Distribution range (ha)	Number of fragments	References
150 000	1	De Poorter and Van der Loo (1979)
140 000[a]	1	Hall (1981)
50 000[a]	3	Granados (1981)
27 000	3	López-Forment and Cervantes (1981)
28 000	4	Bell et al. (1985)
28 000	4	Hoth et al. (1987)
38 650	16	Velázquez et al. (1991)

[a] Values estimated from the reference since they were not literally given.

The map of Velázquez et al. (1991) permits accurate illustration of the actual man-made habitat fragmentation of the rabbit (Fig. 1). The distribution units given by Velázquez et al. (1991) were considered as isolated populations, since interpopulation genetic flow seems unlikely. This was mostly attributed to intensive human activities such as farming, grazing, burning, and timbering. Furthermore, roads and human settlements serve as barriers to existing rabbit populations.

Regarding ecological fragmentation, six habitat types were identified. The characteristic preferential plant species were used to name the habitat types as follows: habitat 1, alpine bunch-grassland *(Arenaria bryoides-Festuca livida-Calamagrostis tolucensis);* habitat 2, open pine woodland *(Pinus hartwegii-Festuca tolucensis);* habitat 3, mixed alder-pine forest *(Alnus firmifolia-Muhlenbergia macroura);* habitat 4, pine forest (*Pinus* spp.-*Muhlenbergia quadridentata*); habitat 5, open fir forest *(Abies religiosa-Festuca amplissima);* and habitat 6, dense fir forest *(Abies religiosa-Senecio barba-johannis-Cupressus lindleyi).* A detailed description of these habitats and their ecology is given in separate reports Rzedowski 1988; Velázquez et al. 1992; Almeida et al. 1992).

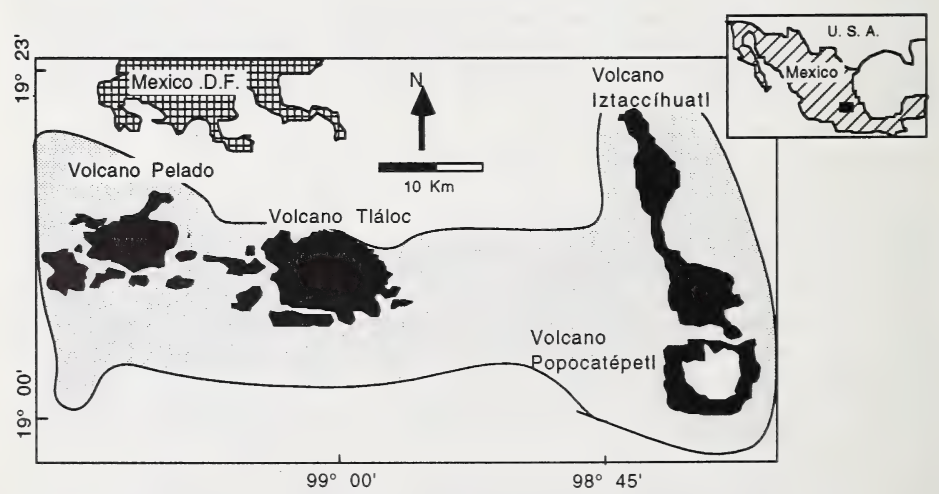


Fig. 1. Comparative distribution ranges of the volcano rabbit *(Romerolagus diazi).* The area hatched with points (□) represents the distribution range given by Hall (1981), which was based on the marginal records. The 16 patches in black (■) are the present distribution areas (Velázquez et al. 1991). All fragments are separated by man-made barriers such as: roads, inhospitable habitats, and human settlements. Therefore, inter-population genetic flow between the 16 fragments inhabited by *Romerolagus* seems unlikely

Table 2. **Matrix of canonical correlation coefficients**

The ordination of the habitat types is represented by the species axes. The variable axes are given as explanatory variables of the distribution of the habitat types. The actual ecological amplitude is shown in the ordination diagram (Fig. 2)

	Species axis I	Species axis II	Variables axis I	Variables axis II	Ground layer
Species axis I	1				
Species axis II	0.045	1			
Variables axis I	0.950[a]	0	1		
Variables axis II	0	0.834[a]	0	1	
Ground-layer	0.8	−0.154	0.855[a]	−0.185	1
Herb-layer	−0.622	0.339	−0.663	0.407[a]	−0.565
Tree-layer	0.836[a]	−0.001	0.893[a]	0	0.643
Rocks	−0.143	0.059	−0.152	0.071	−0.139
Bare ground	−0.122	0.063	−0.131	0.076	−0.123
Altitude	−0.191	−0.518[a]	−0.204	−0.622[a]	0.026
Rabbit abundance	−0.273	0.08	−0.292	0.095	−0.165

	Herb layer	Tree layer	Rocks	Bare ground	Altitude
Herb-layer	1				
Tree-layer	−0.526	1			
Rocks	0.07	−0.145	1		
Bare ground	0.11	−0.282	0.055	1	
Altitude	0.005	−0.087	−0.097	0.116	1
Rabbit abundance	0.43	0.316	0.064	0.335	0.032

[a] Significant at $P < 0.05$.

The canonical correlation coefficient between first species axis and the first variable axis (r, 0.95), allowed reliable ecological elucidation to explain the distribution of the habitat types. This result was obtained by CCA (Tab. 2). The distribution of the six habitat types is explained mostly by the altitude (axis I, $\lambda = 0.293$) and by the percentage of tree cover (axis l, $\lambda = 0.737$). These two variables explained 71 % of the total variation (51 % percentage of tree cover and 20 % altitude). The Student-T exploratory test shows that the percentage of tree cover contributes significantly to the regression along the first axis ($T = 5.98$; d. f. 105; $P < 0.05$), as well as the ground-layer coverage ($T = 3.60$; d. f. 105; $P < 0.05$). The altitude ($T = 4.71$) and the herb-layer ($T = 3.90$) contributed significantly to the regression of the second axis. The 20 random data-set generated by "Monte Carlo Permutation Test" yielded lower "eigenvalues" than the ones obtained by the ordination analysis. This result indicates that the canonical ordination analysis could not have been obtained by chance only ($P < 0.05$).

The characteristic preferential species of the six habitat types and the variables (arrows) included in the analysis are shown in the ordination diagram (Fig. 2). In this figure, it can be observed that habitat types 2 and 3 were positioned rather close to each other near the center of the ordination diagram. At the right end of the first axis, habitat types 5 and 6 were also positioned relatively close. Clustering of habitat types along the ordination axis suggests that these habitats are distributed along similar ecological conditions (Ter Braak 1987, 1988). Furthermore, the herb-layer seems to play an important role in determining the ecological amplitude of habitat 2. In relation to the rabbit distribution, the canonical correlation coefficient of the tree-layer and herb-layer reached the highest scores (−0.526 and 0.430, respectively). Tree-layer and herb-layer were the variables that explained most of the distribution and relative abundance of the rabbit (Tab. 2). On the other hand, the

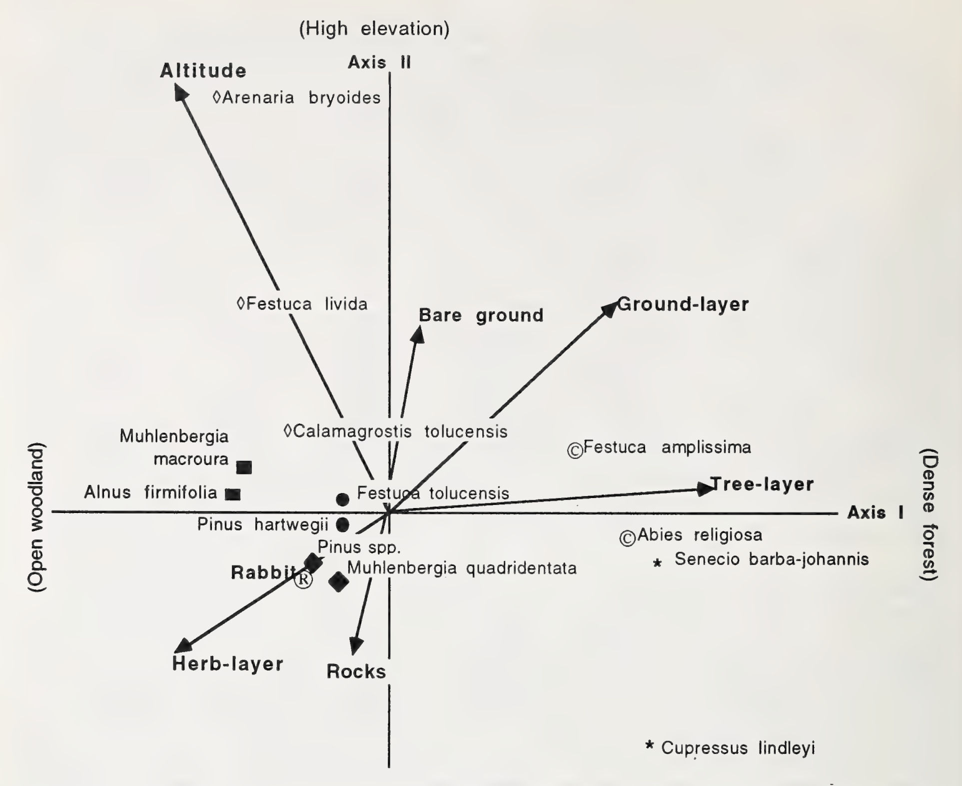


Fig. 2. Ordination diagram of the habitat types present in the distribution range of the volcano rabbit *(Romerolagus diazi)* obtained by Canonical Correspondence Analysis ($\lambda 1 = 0.737$; $\lambda 2 = 0.293$; scaling $\alpha = 1$). Habitat 1 (◇) = alpine bunch-grassland *(Arenaria bryoides-Festuca livida-Calamagrostios tolucensis);* habitat 2 (●) = open pine woodland *(Pinus hartwegii-Festuca tolucensis);* habitat 3 (◆) = mixed alder-pine forest *(Alnus firmifolia-Muhlenbergia macroura);* habitat 4 (■) = pine forest (*Pinus* spp.-*Muhlenbergia quadridentata*); habitat 5 (©) = open fir forest *(Abies religiosa-Festuca amplissima);* and habitat 6 (★) = dense fir forest *(Abies religiosa-Senecio barba-johannis-Cupressus lindleyi)*

centroid of the variable rabbit (®) is positioned within the ecological amplitude of habitats 2, 3 and 4. This suggests that habitat types 2 and 3 are indicative of the most suitable environmental conditions for the volcano rabbit. In other words, the abundance of the rabbit is restricted due to environmental conditions in habitat types 1, 5, and 6. Finally, the present mosaic of habitats and their relation to the rabbit abundance demonstrates ecological fragmentation.

Discussion

In Mexico split habitats of mammalian species distributed along large areas is commonly observed (Leopold 1965; Hall 1981). The actual causes of the scattered distribution of such species is rarely documented. Human activities, environmental discontinuities, or by both factors can work simultaneously in promoting insularization (Wilcox 1980; Wilcove 1986). It is necessary to distinguish the actual cause of fragmentation for conservation and management actions (Diamond 1984; Simberloff and Abele 1984). Man-made fragmentation is certainly easy to detect, unlike ecologial fragmentation which requires detailed knowledge of the habitat and the abundance of the species. Reliable density

estimates are unknown for most mammalian species, which limits proper habitat assessment studies (Van Horne 1983). In this research relative abundance estimates provided sufficient data to document the actual ecological amplitude of the volcano rabbit. Taking into account volcano rabbit presence only all habitat types are occupied except number 6 (dense fir forest characterized by *Abies religiosa-Cupressus lindleyi).* This suggests that actual ecological amplitude cannot be found through presence-absence data only (Velázquez et al. 1992). Therefore, abundance estimates are recommended to find ecologically sound relations between habitat and mammalian species. Furthermore, conservation plans ought to be base upon the actual ecological amplitude of the species.

A large number of studies have documented the impact of habitat fragmentation in bird populations (Nilsson 1978; Haila and Hanski 1984; Robbins 1979; Whitcomb et al. 1981; Lynch and Whigham 1984). This contrasts with the number of studies on habitat fragmentation in populations of mammals (Smith 1974; Velázquez et al. 1991). Interannual variability of the density in mammalian populations (Krebs et al. 1973) influences its distribution. Seasonal periods (winter-summer or rainy-dry) promote movement of mammalian populations between habitats (Kikkawa 1964; Churchfield 1980). Hence, heterogeneous landscapes are needed to fulfill all requirements for survival (Hansson 1979; Alcantara and Telleira 1991). Lagomorphs inhabit a broad range of ecologically diverse environments including disturbed, successional, and transitional habitats (Chapman and Flux 1990). Nevertheless, the urgent protection of five genera (among them *Romerolagus*) is demanded. This is mainly due to the small distribution area and specific habitat requirements of the genera (Chapman and Flux 1990). To illustrate this further, pikas *(Ochotona)* store food in caches (haypiles) which serve as a source of energy for the winter, together with other cushion plants (Smith et al. 1991). This, therefore, suggests that pika population movement between habitats is not necessary during periods of food-shortage. Personal observations of the volcano rabbit seem to suggest a rather stable microclimatic environment (beneath of the bunch-grass). This might be due to the coverage provided by the bunch-grass, which in summer is cooling and in winter warming. Therefore, it seems unlikely that the populations of volcano rabbits move between different habitats in different seasons. This, however, remains to be ascertained.

Acknowledgements

The author thanks F. J. Romero, J. López-Paniagua, L. León for their assistance in the field and continuouis discussions, which enriched the paper. C. J. Krebs and C. Galindo-Leal provided help with the data analysis. A. M. Cleef and P. J. H. van Bree encouraged the publication of the data included in this paper. J. L. Hinton and E. Zwiep helped improving the linguistics.

Zusammenfassung

Anthropogene und ökologische Lebensraumverinselung am Beispiel des Vulkankaninchens (Romerolagus diazi)

Die Verinselung des Lebensraumes für das mexikanische Vulkankaninchen *(Romerolagus diazi)* wird dokumentiert. Dabei werden zwei unterschiedliche Prozesse beleuchtet: anthropogene und ökologische Fragmenation. Der Mensch zerteilt den Lebensraum in Inseln durch den Bau von Autobahnen, durch Ackerbau, intensives Abflämmen und Weidenutzung. Ökologische Verinselung ist auf Diskontinuitäten der Umgebung, die in einem Mosaik von Pflanzen und Habitaten resultieren, zurückzuführen. 6 Habitat-Typen werden unterschieden. Davon bieten zwei, der offene Tannenwald *(Pinus hartwegii – Festuca tolucensis)* und der Tannenwald (*Pinus* spp. – Muhlenbergia macroura), die günstigsten ökologischen Bedingungen für das Überleben des Vulkankaninchens. Die zwei genannten Prozesse der Habitatverinselung bedrohen sein Überleben. Diese Prozesse werden im Hinblick auf ihre Rolle bei der Erhaltung und dem Management der Art besprochen .

References

Alcantara, L.; Telleira, F. (1991): Habitat selection of the Wood mouse *(Apodemus sylvaticus)* in cereal steppes of Central Spain. Z. Säugetierkunde **56,** 347–351.

Almeida, L.; Cleef, A. M.; Herrera, A., Luna, I.; Velázquez, A. (1992): El zacatonal alpino de la vertiente NW del Volcán Popocatépetl, México. Phytocoenologia (submitted).

Bell, D.; Hoth, J.; Velázquez, A.; Romero, F. J.; León, L.; Aranda, M. (1985): A survey of the distribution of the volcano rabbit *Romerolagus diazi,* an endangered mexican endemic. Dodo, J. Jersey Wildlife Preserv. Trust Intern. **22,** 12–18.

Braun-Blanquet, J. J. (1951): Pflanzensoziologie, Grundzüge der Vegetationskunde. 2nd Ed. Vienna, New York: Springer.

Ceballos, G.; Galindo, C. (1984): Mamíferos silvestres de la Cuenca de México. México: Limusa.

Cervantes, F. A.; Martines, V. J. (1992): Historia natural del conejo zacatuche. In: El conejo zacatuche *(Romerolagus diazi)* y su habitat. Ed. by A. Velázquez; F. J. Romero and J. López-Paniagua. México: Editorial, UAM. (In pres).

Chapman, J. A.; Flux, J. E. C. (1990): Introduction and overview of the lagomorphs. In: Rabbits, Hares, and Pikas. Status survey and conservation action plan. Ed. by J. A. Chapman and J. E. C. Flux. Gland, Switzerland: IUCN-The World Conservation Union and World Wide Fund for Nature. Pp. 1–6.

Churchfield, S. (1980): Population dynamics and the seasonal fluctuations in numbers of the common shrew in Britain. Acta Theriol. **25,** 415–424.

De Poorter, M.; Van der Loo, W. (1979): Le lapin de Diaz ou teporingo. Zoo Anvers, Societé Royale de Zoologie de Anvers **45,** 15–19.

Diamond, J. M. (1984): "Normal" extinctions of isolated populations. In: Extinctions. Ed. M. H. Nitecki. Chicago: University of Chicago Press. Pp. 191–246.

Gibb, A. J. (1970): An experiment in rabbit control. New Zealand J. of Agriculture **120** (5), 28–31.

Granados, H. (1991): Some basic information on the volcano rabbit. In: World Lagomorph Conference. Ed. by K. Myers and C. D. MacInnes. Guelph, Ontario: University of Guelph.

Haila, Y.; Hanski, I. K. (1984): Methodology for studying the effect of habitat fragmentation on land birds. Ann. Zool. Fennici, **21,** 393–397.

Hall, E. R. (1981): The mammals of North America. Vol. 1. 2nd. ed. New York: John Wiley.

Hansson, L. (1979): On the importance of landscape heterogeneous in northern for the breeding population densities of homeotherms: a general hypothesis. Oikos **33,** 182–189.

Harris, L. D. (1984): The fragmented forest: Island biogeography theory and the preservation of biotic diversity. Chicago: University of Chicago Press.

Hill, M. (1979): TWINSPAN-A FORTRAM Program for Detrended correspondence analysis and reciprocal averaging. Ithaca, N.Y.: Cornell University Press.

Hill, M. O.; Gauch, H. G. Jr. (1980): Detrended Correspondence Analysis: an improved ordination technique. Vegetatio **42,** 47–58.

Hoth, J.; Velázquez, A.; Romero, F. J.; León, L.; Aranda, M.; Bell, D. J. (1987): The volcano rabbit: a shrinking distribution and a threatened habitat. Oryx **21,** 85–91.

Kikkawa, J. (1964): Movement activity and distribution of small rodents *Clethrionomys glareolus* and *Apodemus sylvaticus* in woodland. J. Anim. Ecol. **33,** 259–299.

Krebs, C. J.; Gaines, M. S.; Keler, B. L.; Myers, J. H.; Tamarin, R. H. (1973): Population cycles in small rodents. Science **179,** 35–41.

Krebs, C. J.; Gilbert, B. S.; Boutin, S.; Boonstra, R. (1986): Estimation of snowshore hare population density from turd transects. Can. J. Zool. **65,** 565–567.

Leopold, A. S. (1965): Fauna silvestre de México. I. M. R. N. R., México.

López-Forment, W.; Cervantes, R. F. (1981): Preliminary observations on the ecology of *Romerolagus diazi* in Mexico. In: World Lagomorph Conference. Ed. by K. Myers and C. D. MacInnes. Guelph, Ontario: University of Guelph.

Lynch, J. F.; Wingham, D. F. (1984): Effects of forest fragmentation on breeding bird communities in Maryland, U.S.A. Biol. Conserv. **28,** 287–327.

Nilsson, S. G. (1978): Fragmented habitats, species richness and conservation practice. Ambio. **7,** 26–27.

Oosterveld, P. (1983): Eight years of monitoring rabbits and vegetation development on abandon arable fields grazed by ponis. Acta Zool. Fennica **174,** 71–74.

Robbins, C. S. (1979): Effect of forest fragmentation on bird populations. In: Management of Northcentral and Northeastern Forest for nongame birds. Ed. by R. M. DeGraaf. Proc. workshop, U.S. Dept. Agriculture. General technical rep. NC-51.

Rzedowski, J. (1988): Vegetación de México: Limusa.

Simberloff, D.; Abele, L. B. (1984): Conservation and obfuscation: Subdivision of reserves. Oikos **42,** 399–401.

Smith, A. T. (1974): The distribution and dispersal of pikas: consequences of insular population structure. Ecology **55,** 1112–1119.

Smith, A. T.; Formozov, N. A.; Hoffman, R. S.; Zheng Changlin; Erbajeva, M. A. (1991): The Pikas. In: Rabbits, hares, and pikas. Status survey and conservation action plan. Ed. by J. A. Chapman and J. E. C. Flux. Gland, Switzerland: IUCN-The World Conservation Union and World Wide Fund for Nature. Pp. 14–60.

Soule, M. E. (1986): Conservation Biology. Science of scarcity and diversity. Sunderland, Mass.: Sinauer Ass.

Ter Braak, C. J. F. (1986): Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology **67**, 1167–1179.

— (1987): The analysis of vegetation-environment relationships by canonical correspondence analysis. Vegetatio **69**, 69–77.

Ter Braak, C. J. F. (1988): CANOCO-A FORTRAM program for canonical community ordination by partial detrended canonical correspondence analysis, principal component analysis, and redundancy analysis. Wageningen: TNO Inst. Appl. Computer Sci.

Van Horne, B. (1983): Density as misleading indicator of habitat quality. J. Wildl. Manag. **47**, 893–901.

Velázquez, A. (1992): Geo-ecología del volcán "Pelado", México: estudio enfocado hacia la conservación del conejo zacatuche. In: El conejo zacatuche *(Romerolagus diazi)* y su habitat. Ed. by A. Velázquez, F. J. Romero and J. López-Paniagua. México: Editorial, UAM. (In press).

Velázquez, A.; Romero, F. J.; León, L. (1991): Estudios sobre la distribución y fragmentación del habitat del zacatuche (*Romerolagus diazi:* Ferrari-Pérez, 1893). Resumen 63, I Cong. Nac. de Mazto., AMMAC A. C. 7–9 nov., Xalápa, Veracrúz, México. Pp. 37–38.

Velázquez, A.; Romero, F. J.; López-Paniagua, J. (1992): Amplitud y utilización del habitat del conejo zacatuche. In: El conejo zacatuche *(Romerolagus diazi)* y su habitat. Ed. by A. Velázquez, F. J. Romero and J. López-Paniagua. México: Editorial, UAM. (In press).

Whitcomb, B. L.; Whitcomb, R. F.; Bystrak, D. (1981): Island biogeography and "habitat islands" of eastern forest. Part III. Long-termo turnover and effects of selective logging on the avifauna of forest fragments. Am. Birds **31**, 17–23.

Whittaker, R. H. (Ed.) (1973): Ordination and classification of communities. Handbook of vegetation science. The Hague: Junk.

Wilcove, D. S.; Mclellan, C. H.; Dobson, A. P. (1986): Habitat fragmentation in the temperate zone. In: Conservation Biology. Science of scarcity and diversity. Ed. by M. E. Soulé. Sunderland, Mass.: Sinauer Ass. Pp. 237–256.

Wilcox, B. A. (1980): Insular ecology and conservation. In: Conservation Biology. Science of scarcity and diversity. Ed. by M. E. Soulé. Sunderland, Mass.: Sinauer Ass. Pp. 95–117.

Author's address: M. Sc. J. Alejandro Velázquez Montes, Hugo de Vries Laboratory, University of Amsterdam, Kruislaan 318, NL-1098 SM Amsterdam, The Netherlands

Einladung

Die 67. Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde e.V. findet vom Sonntag, den 26. September, bis Freitag, den 1. Oktober 1993, gemeinsam mit der Jahrestagung der Gesellschaft für Primatologie in Tübingen statt. Gastgeber ist das Zoologische Institut der Universität Tübingen (Prof. Dr. W. MAIER, Prof. Dr. H.-U. SCHNITZLER).

Vorläufiges Programm

Sonntag, 26. September:		Anreise
	ab 16.00 Uhr:	Vorstandssitzung
	ab 19.00 Uhr:	Zwangloser Begrüßungsabend im Ratskeller, Haaggasse 4
Montag, 27. September:	9.00 Uhr:	Hörsaal N 2 im Hörsaalzentrum auf der Morgenstelle: Grußworte und Eröffnung der Tagung durch den 1. Vorsitzenden
	9.30 Uhr:	Hauptvortrag und Kurzvorträge zum Themenschwerpunkt „Offene Fragen der Phylogenie und Systematik der Großgruppen"
	14.00 Uhr:	Vorträge zum Themenschwerpunkt
	16.00 Uhr:	Posterdemonstration
	17.00 Uhr:	Mitgliederversammlung
	20.00 Uhr:	Filmabend
Dienstag, 28. September:	9.00 Uhr:	Hörsaal N 2 auf der Morgenstelle: Hauptvortrag und Kurzvorträge zum Themenschwerpunkt „Geruchssinn und olfaktorische Kommunikation bei Säugetieren"
	14.30 Uhr:	Kurzvorträge
	17.00 Uhr:	Posterdemonstration
	18.30 Uhr:	Empfang durch den Oberbürgermeister der Stadt Tübingen
	20.00 Uhr:	Geselliger Abend im „Schwärzlocher Hof"
Mittwoch, 29. September:		Gemeinsame Tagung mit der „Gesellschaft für Primatologie"
	9.00 Uhr:	Hörsaal N 2 auf der Morgenstelle: Hauptvortrag und Kurzvorträge zum Themenschwerpunkt „Biologie der Primaten"
	14.30 Uhr:	Kurzvorträge
	17.00 Uhr:	Posterprämierung und Abschluß des wissenschaftlichen Programms
	20.00 Uhr:	Öffentlicher Abendvortrag

Donnerstag, 30. September:		Deutsche Gesellschaft für Säugetierkunde: Exkursion in den „Naturpark Schönbuch"
		AG „Fledermausforschung und Fledermausschutz":
	9.00 Uhr:	Kurzvorträge zum Thema „Biologie und Schutz der Chiroptera"
		Gesellschaft für Primatologie:
	9.00 Uhr:	Hörsaal N 2 auf der Morgenstelle: Kurzvorträge zur Biologie der Primaten.
	17.00 Uhr:	Mitgliederversammlung der „Gesellschaft für Primatologie"
Freitag, 1. Oktober:		Treffen verschiedener Arbeitsgemeinschaften

Alle Interessenten sind zu dieser Tagung herzlich eingeladen. Falls eine persönliche Einladung gewünscht wird, wenden Sie sich bitte an den 1. Vorsitzenden der Deutschen Gesellschaft für Säugetierkunde, Prof. Dr. U. SCHMIDT, Zoologisches Institut, Poppelsdorfer Schloß, W-5300 Bonn 1 (Tel. 02 28/73 54 68; Fax-Nr. 02 28/73 54 58) bzw. an den zuständigen Vertreter der Gesellschaft für Primatologie, Prof. Dr. CARSTEN NIEMITZ, FU Berlin, FB 23; Anthropologie und Humanbiologie Fabeckastraße 15, D-1000 Berlin 33 (Tel. 0 30/8 38 29 00; Fax-Nr. 0 30/8 38 29 00).

Das Programm mit der Vortragsfolge wird den Mitgliedern – auf Anforderung auch Nichtmitgliedern – rechtzeitig vor der Tagung zugesandt. Außer Beiträgen zu den genannten Themenschwerpunkten werden auch dieses Mal wieder Vorträge und Posterdemonstrationen zu anderen Fachgebieten der Säugetierkunde berücksichtigt. Bitte melden Sie Kurzvorträge (15 Min. + 5 Min. Diskussion) sowie Posterdemonstrationen möglichst frühzeitig, spätestens jedoch bis zum 30. April (Ausschlußfrist) beim Geschäftsführer unserer Gesellschaft, Prof. Dr. H. ERKERT, Zoologisches Institut, Auf der Morgenstelle 28, W-7400 Tübingen (Tel. 0 70 71/29 29 58; Fax: 0 70 71/29 46 34) an, und fügen Sie dazu eine maximal einseitige informative Kurzfassung bei.

Mit Fragen zum Tagungsort und zur Organisation wenden Sie sich bitte an Herrn Prof. Dr. W. MAIER, Zoologisches Institut der Universität Tübingen, Auf der Morgenstelle 28, D-7400 Tübingen (Tel. 0 70 71/29 26 13 oder 29 54 87; Fax: 0 70 71/29 46 34).

2. Workshop „Säugetier-Bioakustik"

Am Wochenende 17./18. April 1993 findet in Bonn, Zoologisches Forschungsinstitut und Museum Alexander Koenig, das 2. Arbeitstreffen „Säugetier-Bioakustik" statt.

Nachdem sich der 1. Workshop im Frühjahr 1992 an der Humboldt-Universität zu Berlin überwiegend mit Übersichtsvorträgen zur aktuellen Forschung, zu Problemen der Analyse von Lautsignalen und Fragen der Archivierung von Tierstimmen befaßte, soll ein Schwerpunktthema in Bonn die Struktur von Lautrepertoiren sein. Vorschläge für weitere Themenschwerpunkte sind erwünscht.

Die Workshops sollen Gelegenheiten bieten, alle diejenigen zu einem zwanglosen Gedankenaustausch zusammenzubringen, die Forschungsarbeit über lautliche Kommunikation von Säugetieren betreiben oder planen, Kontakte zu Linguisten, Phonetikern oder Stimmphysiologen sowie Physikern, Elektro-Ingenieuren o. ä. mit akustischen Analysen befaßten Kollegen werden angestrebt.

Insgesamt soll ein Forum geschaffen werden, das Anfängern wie Fortgeschrittenen auf

diesem Arbeitsgebiet die Präsentation laufender Projekte wie vorläufiger Modellvorstellungen ermöglicht und viel Raum für Diskussionen zuläßt.
Für nähere Informationen wenden Sie sich bitte an:

Dr. Gustav Peters
Zoologisches Forschungsinstitut und
Museum Alexander Koenig
Adenauerallee 150–164
W-5300 Bonn 1
Tel.: (02 28) 91 22-2 62,
Fax: (02 28) 21 69 79

oder

Dr. Karl-Heinz Frommolt
Humboldt-Universität zu Berlin
Institut für Verhaltensbiologie
und Zoologie
Invalidenstraße 43
O-1040 Berlin
Tel.: (0 30) 28 97-26 40
Fax: (0 30) 28 97-26 41

Gründung einer „Arbeitsgemeinschaft Bisam“

Diese AG soll ein Forum für alle an der Bisamforschung interessierten und beteiligten Wissenschaftler sein und einem internationalen Daten- und Informationsaustausch dienen. Die 1. Arbeitstagung findet vom 4.–6. April 1993 in Braunschweig statt.
Interessenten können ihre Arbeit in Form eines Kurzvortrags oder eines Posters vorstellen.
Geplanter Tagungsverlauf:

Sonntag, 4. 4. 1993: Ab 17.00 Uhr Öffnung des Tagungsbüros, 20.00 Uhr: Begrüßungsabend.

Montag, 5. 4. 1993: 9.00 – 17.00 Uhr: Kurzvorträge, 17.30 – 19.30 Uhr: Wiss. Beiprogramm, 20.15 Uhr: Geselliger Abend.

Dienstag, 6. 4. 1993: 9.00 – 12.00 Uhr: Kurzvorträge, 13.00 – 17.00 Uhr: Wiss. Beiprogramm.

Tagungsgebühr: 10,– DM. Anmeldungen und Auskünfte bei:
Carsten Bothe, Köterei 15, W-3300 Braunschweig, Tel.: (05 31) 37 31 75.

Erscheinungsweise und Bezugspreis 1993: 6 Hefte bilden einen Band. Jahresabonnement Inland: DM 378,– zuzüglich DM 13,80 Versandkosten; Jahresabonnement Österreich: öS 2940,– zuzüglich öS 140,– Versandkosten; Jahresabonnement Schweiz: sfr 364,– zuzüglich sfr 17,50 Versandkosten; Jahresabonnement EG-Binnenmarkt-Länder mit USt-ID-Nr.: DM 354,– zuzüglich DM 16,82 Versandkosten; Jahresabonnement EG-Binnenmarkt-Länder ohne USt-ID-Nr. und Drittländer: DM 378,– zuzüglich DM 18,– Versandkosten. Das Abonnement wird zum Jahresanfang berechnet und zur Zahlung fällig. Es verlängert sich stillschweigend, wenn nicht spätestens am 15. November eine Abbestellung im Verlag vorliegt. Die Zeitschrift kann bei jeder Buchhandlung oder bei der Verlagsbuchhandlung Paul Parey, Spitalerstraße 12, W-2000 Hamburg 1, Bundesrepublik Deutschland, bestellt werden. Die Mitglieder der „Deutschen Gesellschaft für Säugetierkunde" erhalten die Zeitschrift unberechnet im Rahmen des Mitgliedsbeitrages.

Z. Säugetierkunde 58 (1993) 1, 1–64

Pferdefütterung

Von Prof. Dr. Dr. h. c. Helmut Meyer, Direktor des Instituts für Tierernährung der Tierärztlichen Hochschule Hannover.
2., verbesserte und erweiterte Auflage. 1992. 223 Seiten mit 34 Abbildungen und 97 Tabellen. Gebunden DM 39,80
ISBN 3-489-64732-7

Die zweite Auflage seines erfolgreichen Buches „Pferdefütterung" hat der Autor in allen Kapiteln entsprechend den rasch zunehmenden wissenschaftlichen Erkenntnissen auf diesem Gebiet gründlich überarbeitet und dem neuesten Wissensstand angepaßt. Zusätzlich konnten u. a. Fragen über Haltung, Rassen, Leistungen und Körperzusammensetzung eingehender behandelt werden. Auch einigen speziellen Problemen wie Fütterung der Leistungspferde, Beziehungen zwischen Fütterung und Krankheit oder Ernährung kranker Pferde wurde mehr Raum gegeben. Mit neuen praxisreifen Erkenntnissen erfüllt die Neuauflage alle Ansprüche sowohl von Pferdehaltern mit ihren unterschiedlichen Intentionen, als auch von Tierärzten, Studierenden der Veterinärmedizin und allen an der Pferdeernährung Interessierten.

Aus einer Besprechung der ersten Auflage:

„Wem dieses Buch von Professor Meyer noch unbekannt ist, der sollte schnellstens diese wichtige Fütterungslehre anschaffen. Neben den anatomischen und physiolo-gischen Grundlagen wird sehr ausführlich auf den Bedarf und die Fütterungspraxis vom extensiv gehaltenen Pony bis hin zum Hochleistungspferd eingegangen."

Reiterjournal

Preis: Stand 1. Januar 1992



Berlin und Hamburg

(2), 65–128, April 1993 ISSN 0044-3468 C 21274 F

ZEITSCHRIFT FÜR SÄUGETIERKUNDE

INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Organ der Deutschen Gesellschaft für Säugetierkunde



Verlag Paul Parey Hamburg und Berlin

This journal is covered by Biosciences Information Service of Biological Abstracts, and by Current Contents (Series Agriculture, Biology, and Environmental Sciences) of Institute for Scientific Information

---

Die Zeitschrift für Säugetierkunde veröffentlicht Originalarbeiten und wissenschaftliche Kurzmitteilungen aus dem Gesamtgebiet der Säugetierkunde, Besprechungen der wichtigsten internationalen Literatur sowie die Bekanntmachungen der Deutschen Gesellschaft für Säugetierkunde. Verantwortlicher Schriftleiter im Sinne des Hamburgischen Pressegesetzes ist Prof. Dr. Dieter Kruska.

Zusätzlich erscheint einmal im Jahr ein Heft mit den Abstracts der Vorträge, die auf der jeweiligen Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde gehalten werden. Sie werden als Supplement dem betreffenden Jahrgang der Zeitschrift zugeordnet. Verantwortlich für ihren Inhalt sind ausschließlich die Autoren der Abstracts.

Manuskripte: Manuskriptsendungen sind zu richten an die Schriftleitung, z. Hd. Prof. Dr. Dieter Kruska, Institut für Haustierkunde, Biologie-Zentrum, Neue Universität, Olshausenstr. 40–60, W-2300 Kiel, Bundesrepublik Deutschland. Für die Publikation vorgesehene Manuskripte sollen gemäß den „Redaktionellen Richtlinien" abgefaßt werden. In ihnen finden sich weitere Hinweise zur Annahme von Manuskripten, Bedingungen für die Veröffentlichung und die Drucklegung, ferner Richtlinien für die Abfassung eines Abstracts und eine Korrekturzeichentabelle. Die Richtlinien sind auf Anfrage bei der Schriftleitung und dem Verlag erhältlich.

Sonderdrucke: Anstelle einer Unkostenvergütung erhalten die Verfasser von Originalbeiträgen und Wissenschaftlichen Kurzmitteilungen 50 unberechnete Sonderdrucke. Mehrbedarf steht gegen Berechnung zur Verfügung, jedoch muß die Bestellung spätestens mit der Rücksendung der Korrekturfahnen erfolgen.

Fortsetzung 3. Umschlagseite

Verlag: Paul Parey, Hamburg und Berlin. Anschriften: Spitalerstr. 12, D-2000 Hamburg 1; Seelbuschring 9–17, D-1000 Berlin 42, Bundesrepublik Deutschland. – Printed in Germany by Westholsteinische Verlagsdruckerei Boyens & Co., Heide/Holst.

Z. Säugetierkunde 58 (1993) 65–74

ISSN 0044-3468

Variation in foraging behaviour, habitat use, and diet of Large slit-faced bats (*Nycteris grandis*)

By M. B. Fenton, I. L. Rautenbach, D. Chipese, M. B. Cumming, M. K. Musgrave, J. S. Taylor, and T. Volpers

Department of Biology, York University, North York, Ontario, Canada: Department of Mammalogy, Transvaal Museum, Pretoria, South Africa; Mana Pools National Park, Zimbabwe; Department of Zoology, Rhodes University, Grahamstown, South Africa; Mupandawana, Zimbabwe

Receipt of Ms. 30. 6. 1992
Acceptance of Ms. 6. 10. 1992

Abstract

Examined the diet of *Nycteris grandis*, a 30–35 g African nycterid which varied significantly from year to year, season to season and roost to roost, suggesting flexible foraging behaviour and opportunism. Frogs, insects, and bats formed the bulk of the bats' diet. Although five species of frogs were consumed, two dominated the diet. Insect prey were mainly larger Lepidoptera and Orthoptera with occasional consumption of smaller species (< 10 g) of bats. Diurnal insects (butterflies – Lepidoptera; dragon flies – Odonata) and small (≤ 10 g) birds also were eaten. Over 14 nights in June 1990, prey taken by *N. grandis* did not reflect the availability of frogs, bats or insects. Radio-tagged *N. grandis* showed significant variation in approach to foraging, including the use of woodland or river habitat, and two foraging techniques, namely hunting from continuous flight or from a perch.

Introduction

Variability in prey arises in several circumstances. For example, animals make decisions about factors such as where and when to forage, and what and how much to eat (Cangialoski 1991; Lucas and Walter 1991; Menzel 1991; Valone 1991) which can produce variation in the approach to foraging, patterns of habitat use, and prey selection. Variation in individuals' behaviour and learning also affect foraging (Kamil et al. 1987) contributing to overall patterns of behaviour and habitat use (e.g., Kieffer and Colgan 1991) which often affect diet. Also contributing to varied diets are prey availability (e.g., Schaller 1972; Kruuk 1972) and/or the use of different approaches to hunting sometimes adjusted according to the prey being hunted (e.g., Henry 1986; Mills 1990). Flexibility in hunting behaviour can translate into variation in diet and improved chances of survival, particularly under marginal conditions.

Since most species of animal-eating bats are insectivorous, their prey is much smaller than them. Insectivorous species that hunt from continuous flight and use echolocation to detect and track prey, usually eat airborne insects (Fenton 1990). Variability in the diets of such aerial insectivores appears to reflect prey availability. For example, both the bird, *Chordeiles minor* (common nighthawks), and the bat, *Eptesicus fuscus* (big brown bats) forage from continuous flight and vary their diets according to prey availability (Brigham 1990, 1991). In some bat communities, species-specific approaches to foraging translate into different patterns of habitat use, prey selection and life history (Barclay 1991).

But there are animal-eating bats that use more than one approach to foraging, alternating between foraging from continuous flight or from a perch (Fenton 1990). Among these species, larger bats (e.g., *Nycteris grandis* – Fenton et al. 1990; *Megaderma lyra* – Audet et al. 1991) consume larger prey, including small vertebrates. Bats using more than one approach to foraging and eating a variety of prey represent and opportunity to

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5802-0065 $ 02.50/0

assess interactions between variation in approach to foraging and variation in the prey taken.

Nycteris grandis (Nycteridae) weighs 30–35 g and occurs widely in Africa in rain forest and savannah woodlands (SMITHERS 1983). Along the Zambezi River in Zimbabwe, *N. grandis* eats large arthropods, fish, frogs, birds and bats, and tagged individuals consistently use the same day and night roosts (e.g., FENTON et al. 1990). Previous dietary analyses over 14 months suggested distinct seasonal variation, for example with bats constituting most of the prey biomass in the "winter" (June and July) diet. Radio-tagged bats adjusted their approaches to hunting according to prevailing conditions, sometimes foraging from continuous flight, other times from perches, differences that coincided with variation in habitat use and in prey consumed (FENTON et al. 1990).

This study had three goals: 1. to assess variation in prey over a longer period of time and to explore the prevalence of previously identified seasonal trends; 2. to use a more intensive behavioural study to consider how variation in prey related to prey availability, approach to foraging, and patterns of activity and habitat use; and 3. to determine the circumstances in which other species of bats are prey.

Material and methods

The study area was in Mana Pools National Park in Zimbabwe (15° 44′ S; 29° 21′ E) where prey selection data cover the period from April 1988 to June 1990, the more intensive study was conducted from 15 to 30 June 1990.

Prey selection was determined from remains gathered from beneath two feeding perches, a disused watertower (8 m by 8 m by 20 m) and the verandah outside the park office headquarters. Discarded pieces of prey were collected approximately once a month (April 1988 to 14 June 1990) or every day (15 to 30 June 1990) at feeding perches and the remains were sorted according to number of prey and identified as accurately as possible.

During the period 15 to 30 June 1990, we used radio tracking to monitor habitat use, activity patterns, and foraging behaviour of individual *N. grandis*. We captured five *N. grandis* (three males and two females) in their day roosts and attached 0.9 g Holohil BD-1 transmitters to their mid-backs using Skinbond[r] adhesive. Radio-tagged bats were tracked using AVM LA12 receivers with collapsible five element Yagi antennae. Pairs of observers on foot or single observers in vehicles, in touch by walkie-talkie, tracked tagged bats from 17:45 h (approximately 15 min before dark) to 06:00 h about 30 min after dawn. Most data, however, come from one individual followed throughout 7 nights. Within one day, one female shed her transmitter, and we occasionally followed three other bats. Data about the bat's movements and behaviour were recorded on hand-held cassette recorders, from which we obtained minute-by-minute details about behaviour.

Using a Javelin night vision scope, we observed *N. grandis* roosting in the water tower at night. These observations permitted us to assess the bats' behaviour within the roost, including eating, grooming, and general activity. On four occasions when the large *Nycteris* were roosting in the water tower, we released smaller bats (six *Nycticeius schlieffeni*, one *Eptesicus capensis*) into the water tower. This was done once with one bat during the day, and twice at night with pairs of bats. Behavioural observations were recorded on a cassette tape recorder.

To assess prey availablity, we sampled the flying insects and bats. Flying insects were sampled using a Malaise trap set in woodland approximately 20 m from the south bank of the Zambezi River. The trap was checked daily at dawn and at dusk, and the numbers and identities of insects over one cm long were recorded. We looked and listened for frogs as we moved through the study area radio-tracking bats. Bats were sampled using two techniques. On seven nights at 15 min intervals we simultaneously monitored bat activity for one minute periods. Using Mini-2 Bat Detectors (Ultra Sound Advice, 23 Aberdeen Road, London N5 2UG, England) observers scanned from 20 to 80 kHz, counting trains of echolocation calls as bat passes. On 8 nights we set two 6 m high by 30 m long mist nets (RAUTENBACH 1985) from 18:00 to 20:00 to sample bats active over or near the Zambezi or Mana Rivers, in woodland within 50 m of the Zambezi, in woodland ca 1 km from the Zambezi and at a pan located in mopane woodland (3 km from the Zambezi). Except for the latter site, the dominant species in the woodland was *Acacia albida* with occasional *Trichelia emetica*.

Results

Variation in diet

Between April 1988 and the end of June 1990, we obtained 45 samples of prey consumed by the *N. grandis*, 37 from the water tower (Fig. 1) and 8 from the office. The identities of 1335 prey were determined as precisely as possible and represented 1 unidentifiable fish, 832 frogs (6 species), 14 bats (at least 4 species), 292 Lepidoptera (46 species) and 197 other arthropods (Orthoptera: Acrididae, Tettigoniidae, 5 genera; Mantoidea 2 genera; Coleoptera; Homoptera: Cicadidae; Odonata 1 genus; Coleoptera; Neuroptera; and Solpugida).

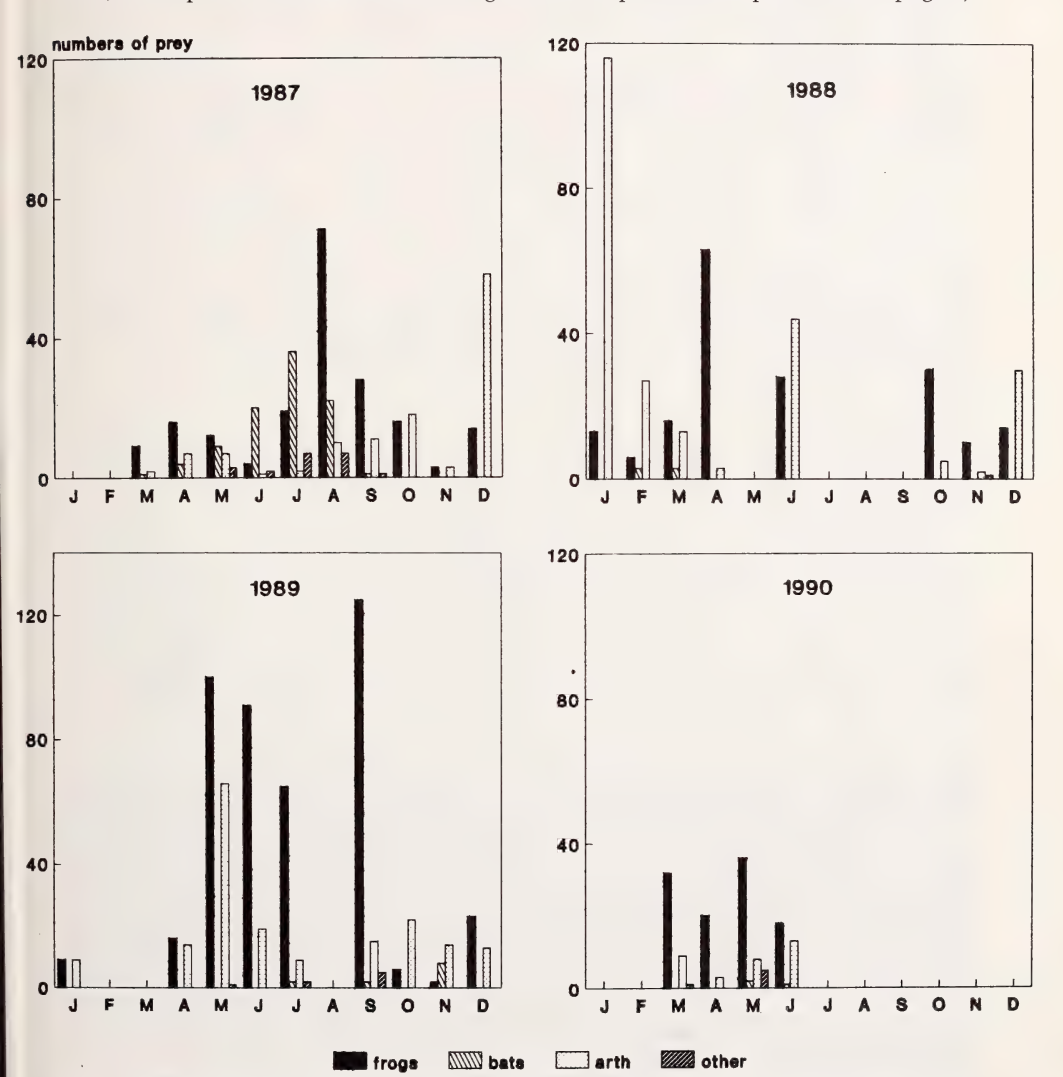


Fig. 1. Four histograms compare the incidence of frogs, bats, arthropods and other prey (fish and birds) in the diet of *Nycteris grandis* using the water tower as a feeding perch in 1987, 1988, 1989 and 1990. The numbers of frogs were determined by counts of legs, bats and birds by counts of wings, fish by counts of tails and arthropods by counts of legs, wings or head capsules. Letters on the horizontal axis indicate months of the year

Nine of 14 bat remains included enough skull material to identify the items as 8 vespertilionids (*Pipistrellus* or *Eptesicus*) and one rhinolophid (probably *Rhinolophus darlingi*). The other five bat remains consisted of wings. Forearms of bat prey ranged from 28–31 mm long (vespertilionids) whereas that of the rhinolophid was 48 mm. These correspond to bat weights of 3–5 g for the vespertilionids and 8–10 g for the rhinolophid (*R. darlingi*; SMITHERS 1983).

Of 832 frogs captured by the bats, 16 % (133) were unidentifiable and 81.2 % (676) were in the genus *Ptychadena* (255 *P. anchietae* and 421 *P. mascariensis*). The bats also had taken 13 *Chiromantis xerampelina*, 7 *Hemisus* (probably *H. marmoratus*, the only species known from the area), 2 *Xenopus muelleri*, and 1 *Tomopterna cryptotis*.

Among the arthropods, moths dominated the diets, although 17 butterflies (14 hesperiids, 2 nympalids, 1 pierid) also were taken. The moths were mainly sphingids and noctuids with some pyralids, geometrids, lymantriids, and saturniids. The distribution of sphingids and noctuids by size (by forewing length) reveals a tendency to take larger species (forewings > 50 mm long), and larger sphingids form a significantly ($\chi^2 = 133$, d.f. = 5, $P \ll 0.001$) larger part of the diet than do large noctuids.

Where possible, we have compared these prey with those reported for 1987 and the earlier part of 1988 (FENTON et al. 1990). Considerable month to month and year to year variation characterizes the diets (Fig. 1). Seasonal trends identified in the 1987 sample (FENTON et al. 1990) are not predictable patterns. This point is demonstrated by statistical comparisons: the incidence of frogs, bats, arthropods, and other prey taken in October, November and December (1987, 1988, and 1989) shows significant variation in the quantities taken among years ($\chi^2 = 108.3$, d.f. = 14, $P < 0.001$); as did the prey taken in April, May and June of 1989 and 1990 ($\chi^2 = 42.27$, d.f. = 12, $P < 0.001$). The incidence of two species of frogs, *Ptychadena anchietae* and *P. mascariensis*, in the March to end of December 1988 samples from the office (46 and 24, respectively) and the water tower (164 and 19, respectively) shows that *N. grandis* using the water tower took significantly more *P. mascariensis* ($\chi^2 = 20.0$, d.f. = 1, $P \ll 0.001$) than those at the office.

Between 15 and 30 June 1990 we could compare prey availability and diet for bats using the water tower as a feeding roost, *N. grandis* consumed 23 prey (4 frogs, one bat and 18 insects). Fifteen of the insects were large (forewing > 50 mm) sphingid moths (*Daphnis nerii* and *Euchloron megaera*). One smaller (wing length 3 cm) sphingid (*Nephele communa*) and two gryllids also were captured. The bats usually brought frogs to their feeding perches during the first hour after dark, while the bat and the sphingids were normally taken between 23:00 and 01:00 h. On 7 consecutive nights starting on 15–16 June 1990, the malaise trap caught 39 insects ≥ 1 cm long (26 moths, 5 mantids, 4 Orthoptera, one Neuroptera, one Trichoptera and two unidentified), but no sphingids. In June 1990, we heard no frogs calling along the river and observed none in 13 nights of walking in the woodland and along the edge of the river. Monitoring the echolocation calls of bats revealed that about 50 % of the activity of species using high intensity echolocation call occurred within the first hour after dark, 80 % in the first three hours. Mist net samples revealed that smaller bats (≤ 10 grams) were abundant and diverse in woodland within 50 m of the river, although the most were encountered at the site farthest from the river (Table 1). The bat captured and eaten by a *N. grandis* during our study and brought to the watertower around midnight, was a rhinolophid or hipposiderid with forearms 48 mm long. Hunting *N. grandis* took prey, insects, frogs and bats that we did not encounter in our sampling.

Variation in behaviour

The male *N. grandis* we followed for 7 entire nights either hunted from a perch or from continuous flight, behaviour reflected by long and short flight times, respectively (Tab. 2). The bat alternated its foraging between the area within 50 m of the river banks and

Table 1. **Captures of bats in mist nets between 18:00 and 20:00 h in different habitats relative to the rivers**

	Mass in g	Over/near water Zambezi	Pan	Woodland < 50 m from River	Woodland > 500 m from	Total
Number of nights		2	1	3	2	8
Epomphorus crypturus	70	0	1	0	1	2
Nycteris thebaica	10	0	0	2	0	2
Rhinolophus hildebrandti	28	0	0	1	0	1
Pipistrellus rueppellii	8	0	0	1	0	1
Eptesicus capensis	5	1	2	0	1	4
Eptesicus zuluensis	4	0	0	1	0	1
Eptesicus cf. *melckorum*	6	1	2	0	0	3
Eptesicus rendallii	7	1	0	0	1	2
Nycticeius schlieffeni	5	0	37	14	5	56
Scotophilus borbonicus	18	13	28	6	5	52
Chalinolobus variegatus	8	1	0	4	1	6
Miniopterus schreibersii	7	0	0	1	0	1
Tadarida pumila	10	0	0	3	0	3
Totals		17	70	33	14	134

Table 2. **The numbers of flights of different durations made by radio-tagged male *Nycteris grandis* within 50 m of the Zambezi River (R) or in woodland (W) on different dates in June**

The dates indicate the day at the beginning of the night

Flight	19 June		21 June		23 June		24 June		25 June		26 June		27 June	
	R	W	R	W	R	W	R	W	R	W	R	W	R	W
≤ 2 min	0	4	4	22	4	1	2	7	13	2	2	0	2	0
3–5 min	1	7	1	3	0	4	0	3	2	4	1	2	2	0
6–10 min	1	3	1	2	0	3	0	2	2	2	2	0	3	0
> 10 min	1	2	0	1	0	0	0	3	2	1	1	0	3	0
Lost contact Time in min	5		8		9		40		65		5		7	
Average flight Time in min	7.3	5.6	2.7	2.5	1.8	6.3	0.8	5.0	3.5	5.2	6.2	4.5	8.5	0

woodland up to 2 km south of the river. Analysis of the numbers of flights of different duration by this male revealed significant night-to-night variation in flight behaviour (χ^2 = 37.2, d.f. = 18, P $<$ 0.001) and habitat use (river versus woodland; χ^2 = 51.5, d.f. = 39, P $<$ 0.001). On most nights the bat began foraging along the river flying there from a disused military bunker less than 50 m from the river or from a 2 km distant hollow *Acacia albida*. Each night it visited the river at least briefly, but on some nights never hunted in the woodland away from the river (Tab. 2). In both habitats the bat used both approaches to hunting. There was no evidence that roost location (*Acacia* versus bunker) affected the bat's choice of foraging areas.

The radio-tagged *N. grandis* showed a peak in flight activity in the hour following dark and, on 5 of 7 nights, another peak between 23:00 and 01:00 (Fig. 2). Over five nights we were in contact with a second radio-tagged male *N. grandis* for a total of 20 h, and this individual showed the same general patterns of flight behaviour and habitat use as the individual we studied intensively.

Radio signals suggested that *N. grandis* roosted motionless in night roosts for long periods of time, an impression supported by 12 h of direct observation of these bats

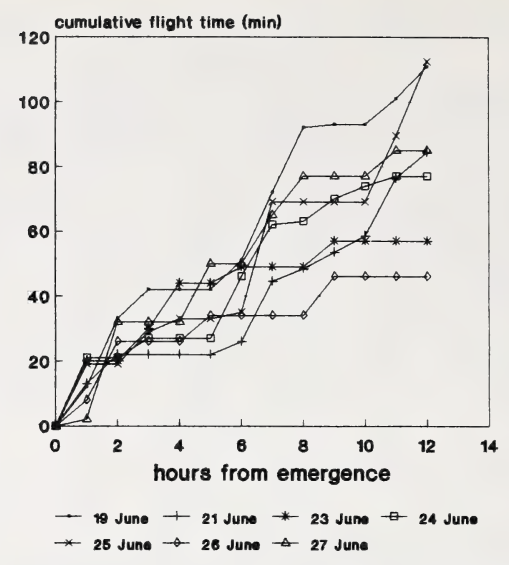


Fig. 2. The differences in patterns of flight times reflect foraging and are illustrated by variation in cumulative flight times (in minutes) for a single bat over 7 nights in June 1990. The dates are identified as follows: 19th = night of 19–20 June, 21st = night of 21–22 June, etc

roosting in the watertower on three nights. After feeding, bats usually groomed themselves and, about once an hour, shifted position within the roost, by either flexing its wings and rotating on the perch, or by flying about 1 m to a different perch. When a *N. grandis* arrived in the watertower, it typically landed away from any others already there. On three occasions (3, 5 and 7 min after arriving) a new bat flew a short distance and roosted about 10 cm from one already in the watertower. Twice, we observed bats arriving with food: they ate their prey and groomed before approaching other *N. grandis*.

Bats as prey

In June 1990, small vespertilionid bats were common in the vicinity of the watertower during our intensive study, but we found no evidence of their being captured by the *N. grandis* (unlike the situation in this exact location in 1987). One explanation for this difference is that they take only bats that fly into their night roost. This explanation is possible in that we twice saw smaller bats fly into the watertower when *N. grandis* was roosting there.

To test this possibility, we released small vespertilionids into the watertower when at least one *N. grandis* was present. During each release, both doors to the water tower were open so small bats could escape. Our single daytime release of a *Nycticeius schlieffeni* elicited no response from the single roosting *N. grandis*, although the small bat flew about the water tower and was conspicuous by its wing flapping and echolocation calls. In contrast, every time we released a small bat into the water tower at night, the roosting *N. grandis* attacked it. In preparation for an attack, a roosting *Nycteris* would partly open its wings and dive towards the flying or roosting bat. The *N. grandis* appeared to vocalize before it left its perch to pursue a bat. During attacks, the smaller bats typically also produced calls audible to human observers in addition to their echolocation calls. The intensity of the attacks ranged from a few passes at the smaller bat, to repeated and

persistent attacks for over 30 min. Small bats that had landed and were motionless on the tower wall never were attacked.

The typical attack rate was 1 every 2 minutes with each attack lasting about 30 sec. One prolonged attack lasted about one minute. The *N. grandis* returned to its perch between attacks and when two *Nycteris* simultaneously were in the tower, one bat usually made several attacks before the other one joined in. None of the ca. 75 attacks we witnessed was successful, and the smaller bats flew out through an open door. The *N. grandis* never pursued the small bats out of the watertower. Bat-eating by *N. grandis* does not appear to be an accidental occurrence generated by other bats straying into roosts occupied by the larger bats.

Discussion

Our results illustrate annual, seasonal and locational variation in prey taken by *N. grandis*, as well as variation in habitat use and approach to foraging. The general patterns of variation in diet are consistent with the general trends previously published for this bat (Fenton et al. 1987), but not with the seasonal diet portrayed by Fenton et al. (1990). The variations in foraging behaviour and habitat use we documented by radio-tracking resemble those reported elsewhere (Fenton et al. 1987; Fenton et al. 1990). Taken together, the patterns of variation indicate that *N. grandis* is opportunistic in its use of prey, habitats and approach to foraging. The combination of behavioural flexibility and access to the large Zambezi River which flows throughout the year may account for the occurrence of *N. grandis* in Zimbabwe, the southern edge of its range (Smithers 1983).

Comparison of the short term information about prey availability and prey captured suggests that *N. grandis* rely on some mechanism(s) to locate preferred targets. For example, although the bats take large noctuids and sphingids, other large moths such as saturniids or lasiocampids are conspicuously absent from the diet. Similarly, the *N. grandis* capture some 5–10 g bats that are common (*Eptesicus* or *Pipistrellus*) but not others (e.g., *Nycticeius schlieffeni*). Also absent from the diet are less common species with diagnostic wing patterns (e.g., the white-winged *Eptesicus rendalli*, the variegated winged *Chalinolobus variegatus*). Absent from the 1989 and 1990 samples were other species in the genus *Nycteris*, which had been a regular prey item in 1987 and early 1988 (recognizeable by the distinctive t-shaped tail cartilage).

The frogs the bats ate also suggest a variety of approaches to hunting (Passmore and Carruthers 1979; D. G. Broadley, pers. comm.). The two *Ptychadena* species show different patterns of escape behaviour, moving towards the water (*P. mascariensis*) or away from it (*P. anchietae*) in the face of danger. *Hemisus* is non-aquatic, living in burrows in the litter by day, while *Chiromantis* is arboreal and cryptic. *Tomopterna* only visits the water to breed and *Xenopus* is virtually entirely aquatic.

The bats could have achieved their selection of prey by using particular foraging flight paths or hunting perches in certain areas. This pattern also could reflect habitat selection by the prey. The radio-tracking data from this and other studies (e.g., Fenton et al. 1987; Fenton et al. 1990) demonstrate that individuals consistently hunt in the same areas, varying their pattern of use of woodland versus the areas along and over the river. In other predators, different approaches to foraging often produce different prey. For example, Henry (1986) found that using different approaches to foraging in the same areas resulted in the capture of different prey by red foxes, and Kruuk (1972) had previously demonstrated this for spotted hyaenas.

Nycteris grandis sometimes use prey-generated sounds to find their targets, whether insects, frogs or other bats, but unlike the Neotropical *Trachops cirrhosus* (Tuttle and Ryan 1981), *N. grandis* shows no sign of locating frogs by listening to their calls (Fenton et al. 1983). *Nycteris grandis* behaves like *Cardioderma cor* from east Africa (Ryan and

Tuttle 1981), using sounds associated with movement to locate its prey. The bats eaten by *N. grandis* include both high (*Eptesicus, Pipistrellus,* and *Rhinolophus*) and low intensity echolocators (*Nycteris*) but the available data do not indicate whether or not *N. grandis* uses the echolocation calls of its bat prey to find these victims.

Some of the prey suggests that *N. grandis* occasionally exploit animals that have been flushed or disturbed. Specifically, butterflies and dragon flies typically stop flying before *N. grandis* emerges, and do not begin flying until after *N. grandis* have returned to their roosts for the day. Exploiting flushed or disturbed prey also could explain the diurnal birds eaten by the bats (Fenton et al. 1981, 1990). The consistent low incidence of diurnal prey suggests that its use is more opportunistic than the result of an active foraging technique. This explanation does not appear to apply to the bats eaten by *N. grandis.*

The importance of prey availability in determining the actual *N. grandis* diet may be suggested by several aspects of the data. First, the significant variation in the prey remains between feeding perches (this study or Fenton et al. 1990) illustrates that parallel samples from nearby sites differ significantly. These differences are important because telemetry data indicate that individuals consistently use the same feeding perches and foraging areas, but the same individual radio-tagged bats did not use the two feeding perches in 1987 or 1990. Variation in prey availability and individual differences also could explain the differences in diet between roosts and between years. Observational learning which has been reported from other bats (Gaudet and Fenton 1984) and associations between mothers and their young (Vaughan 1976; Vaughan and Vaughan 1987) could account for individual differences in hunting technique and prey selection.

In its approaches to foraging, habitat use and prey selection, *Nycteris grandis* resembles other large animal-eating bats in the families Megadermatidae (Audet et al. 1991; Vaughan and Vaughan 1986; Ryan and Tuttle 1987; Vaughan 1976) and Phyllostomidae (Phyllostomidae – Brooke 1989; Medellin 1988; Belwood 1988; Tuttle and Ryan 1981; Vehrencamp et al. 1977). These bats differ from others (e.g., some Vespertilionidae and Molossidae) that show less flexibility in foraging behaviour (Audet 1990; Hickey and Fenton 1990; Barclay 1989; Brigham 1991; Fenton und Rautenbach 1986; Kronwitter 1988; Rydell 1986; Racey and Swift 1985) or flexible foraging behaviour and a smaller range of prey (Jones 1990; Jones and Rayner 1989; Neuweiler et al. 1987; Belwood 1988; Fenton and Rautenbach 1986). Large animal-eating bats with flexible behaviour are the ones typically referred to as "carnivorous", although the label may be inappropriate because invertebrates may comprise a large part of the diet (Nordberg and Fenton 1988).

Nycteris grandis regularly feeds on larger prey items and shows patterns of variation in approaches to hunting and diet comparable to those of other predators. These variations appear to reflect individual decisions probably based on experience and local conditions.

Acknowledgements

We are grateful to the Director of National Parks and Wildlife of Zimbabwe for permission to perform this research and Assistant Director (Research) Rowan B. Martin for help with logistics. We especially thank Warden F. Buyeye and C. Jakopo for their assistance on site, and G. Kachasu, G. Mtungambera, and N. Chasokera for helping us track the bats at night. Dr. N. H. G. Jacobsen, Herpetologist, Transvaal Provincial Administration, Ms L. Brown (Department of Herpetology, Transvaal Museum), Dr. L. Vari (Entomology, Transvaal Museum), Dr. R. toms (Entomology, Transvaal Museum) identified the prey items, and Dr. D. G. Broadley (National Museums of Zimbabwe) provided us with information about frogs at Mana Pools N. P. We thank L. Acharya, D. Audet, M. B. C. Hickey, M. K. Obrist, U. M. Norberg and D. Pearl for reading and making valuable comments about this manuscript, and M. K. Obrist for helping with translations into German. This research was supported by Natural Sciences and Engineering Research Council (Canada) grants to MBF and by the South Africa Foundation Research Development grant to ILR.

Zusammenfassung

Flexibilität in Jagdverhalten, Gebietsanspruch und Ernährung bei der Großen Schlitznasen-Fledermaus, Nycteris grandis

Das Beutespektrum von *Nycteris grandis*, einer 30–35 g schweren Fledermaus der afrikanischen Familie Nycteridae, variierte signifikant zwischen verschiedenen Jahren sowie in Abhängigkeit von der Jahreszeit und der Kolonie. Dies läßt auf ein flexibles, opportunistisches Jagdverhalten schließen. Der Hauptteil der Beute bestand aus Fröschen, Insekten und Fledermäusen. Von fünf gefressenen Froscharten überwogen zwei in der Nahrung. Nachtfalter (Lepidoptera) und Heuschrecken (Orthoptera) dominierten das Spektrum der verzehrten Insekten. Gelegentlich wurden kleinere Fledermäuse (< 10 g) konsumiert. Tagaktive Schmetterlinge (Lepidoptera), Libellen (Odonata) und kleine Vögel (≤ 10 g) fanden sich ebenfalls in der Nahrung. In 14 Beobachtungsnächten im Juni 1990 ergab sich kein Zusammenhang zwischen der von *N. grandis* eroberten Beute und dem verfügbaren Nahrungsangebot. Telemetrierte Tiere zeigten signifikante Unterschiede in der Art der Nahrungssuche. Die Jagdgebiete lagen in bewaldeten Gebieten sowie in Flußlandschaften. Im Jagdverhalten wechselten die Tiere zwischen der Jagd aus andauerndem Flug und der Ansitzjagd.

Literature

Audet, D. (1990): Foraging behaviour and habitat use by a gleaning bat, *Myotis myotis*. J. Mammalogy, **71**, 420–427.

Audet, D.; Krull, D.; Marimuthu, G.; Smuithran, S.; Singh, J. B. (1991): Foraging strategies and the use of space by the Indian false vampire, *Megaderma lyra* (Chiroptera: Megadermatidae). Biotropica **23**, 63–67.

Barclay, R. M. R. (1989): The effect of reproductive condition on the foraging behaviour of female hoary bats, *Lasiurus cinereus*. Behav. Ecol. Sociobiol. **24**, 31–37.

— (1991): Population structure of temperate zone insectivorous bats in relation to foraging behaviour and energy demand. J. Anim. Ecol. **60**, 165–178.

Belwood, J. J. (1988): Foraging behaviour, prey selection and echolocation in phyllostomine bats (Phyllostomidae). In: Animal sonar: processes and performance. Ed. by P. E. Nachtigall and P. W. B. Moore. New York: Plenum Press. Pp. 601–605.

Brigham, R. M. (1990): Prey selection by big brown bats (*Eptesicus fuscus*) and common nighthawks (*Chordeiles minor*). Am. Midl. Nat. **124**, 73–80.

— (1991): Flexibility in foraging and roosting behaviour by the big brown bat (*Eptesicus fuscus*). Can. J. Zool. **69**, 117–121.

Brooke, A. (1988): Prey selection, foraging and habitat use by *Chrotopterus auritus* in Costa Rica. Bat Res. News **29**, 44.

Cangialosi, K. R. (1991): Attack strategies of a spider kleptoparasite: effects of prey availability and host colony size. Anim. Behav. **41**, 639–648.

Fenton, M. B. (1990): The foraging behaviour and ecology of animal-eating bats. Can. J. Zool. **68**, 411–422.

Fenton, M. B.; Cumming, D. H. M.; Hutton, J. M.; Swanepoel, C. M. (1987): Foraging and habitat use by *Nycteris grandis* (Chiroptera: Nycteridae) in Zimbabwe. J. Zool. (London) **211**, 709–716.

Fenton, M. B.; Gaudet, C. L.; Leonard, M. L. (1983): Feeding behaviour of the bats *Nycteris grandis* and *Nycteris thebaica* (Nycteridae) in captivity. J. Zool. (London) **200**, 347–354.

Fenton, M. B.; Rautenbach, I. L. (1986): A comparison of the roosting and foraging behaviour of three species of African insectivorous bats. Can. J. Zool. **64**, 2860–2867.

Fenton, M. B.; Swanepoel, C. M.; Brigham, R. M.; Cebek, J. E.; Hickey, M. B. C. (1990): Foraging behaviour and prey selection by Large Slit-faced Bats (*Nycteris grandis*; Chiroptera: Nycteridae). Biotropica **22**, 2–8.

Fenton, M. B.; Thomas, D. W.; Saseen, R. (1981): *Nycteris grandis*, an African carnivorous bat. J. Zool. (London) **194**, 461–465.

Gaudet, C. L.; Fenton, M. B. (1984): Observational learning in three species of insectivorous bats. Anim. Behav. **32**, 385–388.

Henry, J. D. (1986): Red fox, the catlike canine. Washington, D. C.: Smithsonian Institution Press.

Hickey, M. B. C.; Fenton, M. B. (1990): Foraging by red bats (*Lasiurus borealis*): do interspecific chases mean territoriality? Can. J. Zool. **68**, 2477–2482.

Jones, G. (1990): Prey selection by the greater horseshoe bat (*Rhinolophus ferrumequinum*): optimal foraging by echolocation? J. Anim. Ecol. **59**, 587–602.

Jones, G.; Rayner, J. M. V. (1989): Foraging behaviour and echolocation of wild horseshoe bats, *Rhinolophus ferrumequinum* and *Rhinolophus hipposideros* (Chiroptera, Rhinolophidae). Behav. Ecol. Sociobiol. **25**, 183–191.

KAMIL, A. C.; KREBS, J. R.; PULLIAN, H. R. (Eds.) (1987): Foraging behaviour. New York: Plenum Press.
KIEFFER, J. D.; COLGAN, P. W. (1991): Individual variation in learning by foraging pumpkinseed sunfish, *Lepomis gibbosus*: the influence of habitat. Anim. Behav. **41**, 603–612.
KRONWITTER, F. (1988): Population structure, habitat use and activity patterns of the noctule bat, *Nyctalus noctula* (Schreb., 1774 (Chiroptera: Vespertilionide) revealed by radio-tracking. Myotis **26**, 23–85.
KRUUK, H. (1972): The spotted hyena. Chicago: Univ. of Chicago Press.
LUCAS, J. R.; WALTER, L. R. (1991): When should chickadees hoard food? Theory and experimental results. Anim. Behav. **41**, 579–602.
MEDELLIN, R. A. (1988): Prey of *Chrotopterus auritus*, with notes on feeding behaviour. J. Mammalogy, **69**, 841–844.
MENZEL, C. R. (1991): Cognitive aspects of foraging in Japanese monkeys. Anim. Behav. **41**, 397–402.
MILLS, M. G. L. (1990): Kalahari hyaenas, the comparative behavioural ecology of two species. London: Unwin Hyman.
NEUWEILER, G.; METZNER, W.; HEIILMAN, U.; RUBSAMEN, R.; ECKRICH, M.; COSTA, H. H. (1987): Foraging behaviour and echolocation in the rufous horseshoe bat (*Rhinolophus rouxi*) of Sri Lanka. Behav. Ecol. Sociobiol. **20**, 53–67.
NORBERG, U. M.; FENTON, M. B. (1988): Carnivorous bats? Biol. J. Linn. Soc. **33**, 383–394.
PASSMORE, N. I.; CARRUTHERS, V. C. (1979): South African frogs. Johannesburg: Witwatersrand University Press.
RACEY, P. A.; SWIFT, S. M. (1985): Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during pregnancy and lactation. I. Foraging behaviour. J. Anim. Ecol. **54**, 205–215.
RAUTENBACH, I. L. (1985): A new technique for the efficient use of macro-mistnets. Koedoe **28**, 81–86.
RYAN, M. J.; TUTTLE, M. D. (1987): The role of prey-generated sounds, vision and echolocation in prey location by the African bat, *Cardioderma cor* (Megadermatidae). J. Comp. Physiol. A**161**, 59–66.
RYDELL, J. (1986): Foraging and diet of the northern bat, *Eptesicus nilssoni* in Sweden. Hol. Ecol. **9**, 272–276.
SCHALLER, G. B. (1972): The Serengeti lion. Chicago: Univ. of Chicago Press.
SMITHERS, R. H. N. (1983): The mammals of the southern African subregion. Pretoria: University of Pretoria Press.
TUTTLE, M. D.; RYAN, M. J. (1981): Bat predation and the evolution of frog vocalizations in the neotropics. Science **214**, 677–678.
VALONE, T. J. (1991): Bayesian and prescient assessment: foraging with pre-harvest information. Anim. Behav. **41**, 569–578.
VAUGHAN, T. A. (1976): Nocturnal behaviour of the African false vampire bat (*Cardioderma cor*). J. Mammalogy **57**, 227–248.
VAUGHAN, T. A.; VAUGHAN, R. P. (1986): Seasonality and the behaviour of the African yellow-winged bat. J. Mammalogy **67**, 91–102.
— — (1987): Parental behaviour in the African yellow-winged bat (*Lavia frons*). J. Mammalogy **68**, 217–223.
VEHRENCAMP, S. L.; STILES, F. G.; BRADBURY, J. W. (1977): Observations on the foraging behaviour and avian prey of the Neotropical carnivorous bat, *Vampyrum spectrum*. J. Mammalogy, **58**, 469–478.

Authors' addresses: M. B. FENTON, J. S. TAYLOR; Department of Biology, York University, North York, Ontario, Canada M3J 1P3; I. L. RAUTENBACH, Transvaal Museum, P.O. Box 413, Pretoria, South Africa; D. CHIPESE, Mana Pools National Park, P.O. Box 6, Karoi, Zimbabwe; M. B. CUMMING (deceased), M. K. MUSGRAVE, Department of Zoology, Rhodes University, Grahamstown, South Africa; T. VOLPERS, Box 5, 170 Mupandawana, Zimbabwe

Z. Säugetierkunde 58 (1993) 75–83

ISSN 0044-3468

Winter habitat selection and feeding habits of polecats (*Mustela putorius*) in the Białowieża National Park, Poland

By W. Jędrzejewski, Bogumiła Jędrzejewska, and M. Brzeziński

Mammal Research Institute, Polish Academy of Sciences, Białowieża, Poland

Receipt of Ms. 10. 8. 1992
Acceptance of Ms. 23. 10. 1992

Abstract

Polecats (*Mustela putorius*), that inhabited the pristine mature forests, were studied by means of snowtracking on 11.2 km^2 during 5 winters (1985/86–88/89 and 1990/91). They preferred wet habitats: riverside ash-alder forests and bog alderwoods. Drier forests (oak-linden-hornbeam and spruce-pine stands) were used by polecats less frequently than would have been expected from their occurrence in the study area. The intensity of polecats' use of habitats changed with winter weather. On relatively warm days (0 to −5 °C) polecat tracks were recorded twice as often in wet forests as in the dry ones. At temperatures from −6 to −10 °C, this ratio approached 1 : 1, and below −10 °C, when most of the running and stagnant waters were frozen, polecat tracks were found in drier forests twice as frequently as in wet forests. The diet of polecats was studied by an analysis of 222 scats collected during 5 winters (1986/87–1990/91). Anurans (mainly *Rana temporaria*) comprised 70 to 98 % of the biomass consumed by polecats and were found in 60 to 95 % of scats. Forest rodents (*Apodemus flavicollis* and *Clethrionomys glareolus*) constituted from 1 to 29 % of the biomass eaten by polecats. The consumption of rodents grew with decreasing winter temperature and increasing numbers of rodents. Snowtracking of individual polecats showed that in wet forests, the polecats moved in close proximity to water courses and searched for anurans, whereas in the drier forests, they hunted rodents, mainly by digging.

Introduction

Polecats were often described as predators inhabiting a variety of habitats (Blandford 1987) and showing a generalistic feeding habit (Rzebik-Kowalska 1972; Brugge 1977; Mermod et al. 1983; Lode 1988, 1990). However, the recent studies by Weber (1989a, b) and Jędrzejewski et al. (1989) showed a high specialization of the polecat in capturing anurans. Earlier, Schaff (1911) observed that a relatively high contribution of amphibians to the polecat diet resulted from its living in wet habitats. The later studies of Danilov and Rusakov (1969), Jensen and Jensen (1972), and Lode (1988) confirmed that polecats often live close to water.

In our studies undertaken in the Białowieża National Park, the autumn-winter diet of polecats and their habitat preferences were investigated in the primeval forest. We endeavoured to explain the relationship between the polecat's diet and its habitat selection. We studied the influence of winter weather and the availability of forest rodents on the polecats' utilization of habitats and food resources. The project covered six winters (1985/86–1990/91) and was part of a long-term research project on predator-prey relationships in the pristine forests of the Białowieża National Park (e.g. Jędrzejewski et al. 1989; Brzeziński et al. 1992).

Study area

The Białowieża National Park (eastern Poland, 23° 55′ E, 52° 45′ N) of 47.5 km^2 is located in the center of the Białowieża Primeval Forest (1,250 km^2). The forest extends on both sides of the Polish-Belarussian border and preserves the remnants of the European temperate lowland forests of boreal

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5802-0075 $ 02.50/0

Table 1. **Characteristics of weather conditions during 6 cold seasons (15 Nov.–15 Apr.) and indices of rodent (*C. g.* – *Clethrionomys glareolus* and *A. f.* – *Apodemus flavicollis*) numbers in autumn in Białowieża Primeval Forest, eastern Poland**

Year	Mean daily temperature (°C)	Mean daily snow cover (cm)	Rodent numbers in autumn (N/100 trap-nights)	
			C. g.	*A. f.*
1985/86	−2.5	19	2.1	6.2
1986/87	−3.6	20	1.8	1.9
1987/88	0.2	8	3.8	3.1
1988/89	2.2	2	3.4	1.0
1989/90	2.5	2	0.8	1.3
1990/91	0.6	4	5.8	8.6

nemoral type. It contains the pristine deciduous, mixed, and coniferous stands composed of oak *Quercus robur*, hornbeam *Carpinus betulus*, linden *Tilia cordata*, maple *Acer platanoides*, pine *Pinus sylvestris*, spruce *Picea abies* and other tree species. Along the small forest rivers grow riverside flood-plain forests (composed of ash *Fraxinus excelsior* and black alder *Alnus glutinosa*, with admixture of elm *Ulmus* spp.). Bogs with stagnant water are covered with alderwoods including black alder and admixtures of spruce. Riverside ash-alderwoods and bog alderwoods cover 14.5 % of the National Park area. More information on the vegetation is given by Falinski (1986). In the Park, hunting and timber exploitation are not allowed; tourism is restricted to a few pedestrian paths. A small stream, the Orłówka (about 5.5 km long, up to 4 m wide and 1.5 m deep), flows through the Park. The northern and western borders of the Park are delimited by two rivers (the Narewka and the Hwoźna) which flow in the open marshy valleys. The water level in the rivers and in the stream varies seasonally, reaching its maximum in spring. The Orłówka often dries up in summer. In winter, the Orłówka freezes, however, unfrozen air-holes can still be found in its middle and lower course, at temperatures below −15 °C. The upper part of the stream freezes completely at about −5 °C.

The density of polecats in the study area was 4–5 adult individuals/10 km^2 in winter (Jędrzejewski and Jędrzejewska 1993).

Białowieża National Park lies in the temperate subcontinental climatic zone (Olszewski 1986). An average daily minimum temperature below 0 °C is recorded from November until the end of March. The average minimum temperature in January is −4.3 °C. The mean snow cover is 18 cm. The snow cover is present for an average of 92 days per year. During the study period (1985/86–1990/91), the winter weather was highly variable (Tab. 1).

Material and methods

Habitat selection

In the winters of 1985/86–88/89 and 90/91, habitat preferences of polecats were studied by snowtracking (the winter of 1989/90 was mostly snowless). Tracking was done on 11.2 km^2, on a grid of transects, totalling 59,250 m. All transects were divided into 50-m sections. During the tracking, conducted 1–2 days after the snowfall, the tracks of polecats crossing the transects were recorded. Altogether, 918.7 km of tracking transects were walked and polecat tracks were found in 245 of 18,374 50-m sections. The habitat description of each 50-m section was made on the basis of a forest community map and was verified in the field. The map represents the forest inventory map which distinguished four different habitats: 1. oak-linden-hornbeam forest (rich deciduous stands on brown soils), 2. spruce-pine forest (coniferous and mixed coniferous stands on drier, sandy soil), 3. ash-alder forest (riverside flood plain forests), and 4. bog alderwood (bog forests in places with stagnant waters).

Diet composition and foraging habits

The study of polecat diet was based on the analysis of 222 scats collected during 5 cold seasons (15 Nov.–15 Apr. 1986/87–90/91). Scats were collected at polecat dens, in known polecat territories on the banks of the Orłówka, during radiotracking, on polecat trails during snowtracking, and from livetraps (information on livetrapping and radiotracking is given in Brzeziński et al. 1992). Scats were analyzed following the standard procedure of Lockie (1959). Prey items were identified by bones, hair, feathers and exoskeletons according to the keys of Pucek (1981), Debrot (1982), März (1987)

and comparative skeletal material. The contribution of various prey groups to the polecat diet was shown as percent occurrence (% O) in all analysed scats and percent of mean biomass (% B) consumed per one scat. For the biomass estimation, the following coefficients of digestibility were used (data on polecats, if not stated otherwise): rodents – 17.8 (ROGER et al. 1991), insectivores – 15.2 (averaged from ROGER et al. 1991; LODE 1990), carcasses of cervids – 15 (JĘDRZEJEWSKI and JĘDRZEJEWSKA 1992; for *Vulpes vulpes*), fish – 25 (FAIRLEY et al. 1987; for *Mustela vison*), birds – 12.4 and anurans – 41.3 (ROGER et al. 1991), insects – 5 (LOCKIE 1961; for *Martes martes*). For each winter, food niche breadth was calculated ($B = 1/\Sigma p_i^2$, where p_i = percent biomass of a particular prey group consumed, after LEVINS 1968).

Data on foraging by polecats were obtained by snowtracking individual animals. During tracking, an observer noted the characteristics of the forest type and all activities of an animal that could be inferred from the traces in the snow. The length of a trail was estimated by pacing; 10,970 m of trail were followed.

Climatic data came from the Białowieża meteorological station. The data on autumn numbers of the forest rodents, *Apodemus flavicollis* and *Clethrionomys glareolus* in the years 1985–90, were kindly granted by Dr. Z. PUCEK (from his long-term trapping of forest rodents in Białowieża National Park).

Results

Winter habitat selection of polecats

The general pattern of habitat selection of polecats is shown in figure 1. The most preferred sites were the wet habitats, riverside ash-alder forest and bog alderwood. Drier forest associations (oak-linden-hornbeam forest and spruce-pine forest) were used less frequently than could have been expected from their occurrence in the study area.

The intensity of utilization of particular habitats by polecats changed with weather conditions. Polecat tracks were recorded on 118 sections (each 50 m long) of tracking transects in oak-linden-hornbeam and spruce-pine forests and on 127 sections in riverside

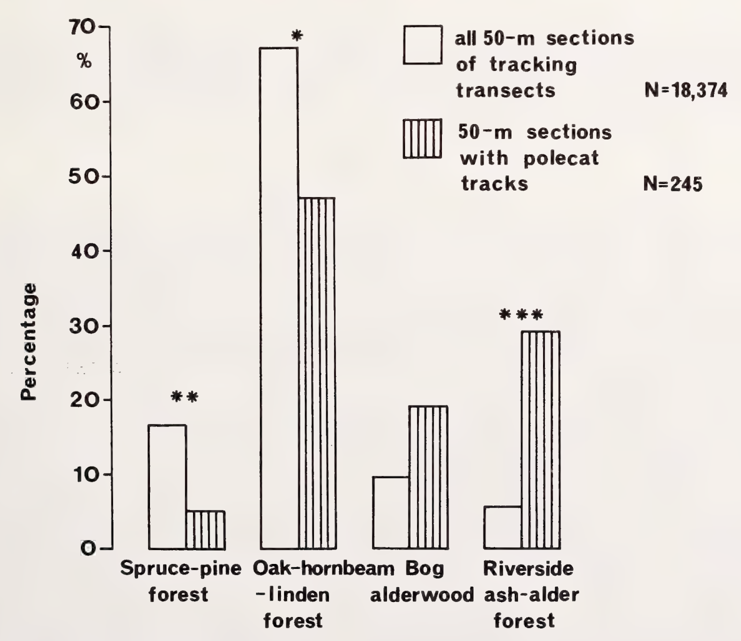


Fig. 1. Winter habitat selection by polecats *Mustela putorius* in the Białowieża National Park, as studied by snowtracking (data pooled for 5 winters, 1985/86–88/89 and 1990/91). * $p < 0.05$, $G = 4.06$; ** $p < 0.01$, $G = 6.72$; *** $p < 0.001$, $G = 17.98$, G-test)

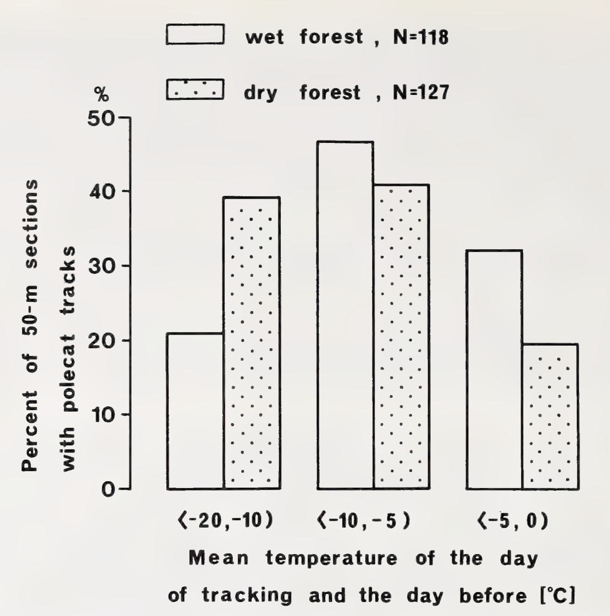


Fig. 2. Use of forest habitats by polecats in winter in relation to temperature as studied by snowtracking. N – number of 50-m sections of tracking transects with polecat tracks recorded. Wet forests – riverside ash-alder forest and bog alderwood, dry forests – oak-hornbeam-linden forest and spruce-pine forest. Frequency distributions statistically different ($p < 0.01$, $t = 2.956$, Wilcoxon test)

and bog forests. At warm temperatures (0 to −5 °C) polecat tracks were recorded twice as often in bog and riverside forests as in the dry forests (Fig. 2). At temperatures from −6 °C to −10 °C, this ratio approached 1 : 1, and below −10 °C, dry forests were utilized twice as often as the completely frozen riverside and bog forests (Fig. 2).

Polecat diet and foraging

In winter, the staple food of polecats was anurans, which comprised 70 to 98 % of the total consumed biomass (Tab. 2). The common frog *Rana temporaria* was most frequently consumed. Rodents, insectivores and ungulate carrion were supplementary foods. The consistently high contribution of anurans to the polecat diet caused the food niche breadth of this predator to be very narrow (1–1.7) with not much variability between winters (Tab. 2).

The lowest contribution of anurans to the polecat diet occurred in 1990/91, when forest rodents were very abundant (see Tab. 1). The share of rodents in the polecat diet increased in years of high rodent densities and during harsh winters. As shown by multiple regression, two variables, average daily temperature in winter (Tw) and index of autumn abundance of forest rodents (Ra), explained 95 % of the variation in the percent occurrence (% O) of rodents in polecat diet in the cold season ($\%O = 8.38 + 1.79Ra - 2.64Tw$, $n = 5$, $F = 18.262$, $R^2 = 0.948$, $p = 0.05$). Variation in rodent abundance contributed more to R^2 than variation in temperature ($sr^2_{Ra} = 60\,\%$, $sr^2_{Tw} = 33\,\%$). The same relationship (although statistically not significant) was recorded for another assessment of the rodent share in polecat diet, percent biomass ($\%B = -6.31 + 2.28Ra - 0.27Tw$, $n = 5$, $F = 6.97$, $R^2 = 0.875$, $p = 0.125$).

Foraging modes of polecats differed among habitats (Tab. 3). In wet forests, polecats

Table 2. **Diet composition (in percent occurrence – % O, and percent biomass – % B) of polecats in the Białowieża National Park in 5 cold seasons (15 Nov.–15 Apr.)**

N – number of scats, B – niche breadth according to LEVINS (1968), + – traces of food, . – biomass not estimated

Item	1986/87 N = 27		1987/88 N = 19		1988/89 N = 95		1989/90 N = 43		1990/91 N = 38	
	% O	% B	% O	% B	% O	% B	% O	% B	% O	% B
Apodemus flavicollis	18.5	3.2	–	–	7.4	1.3	4.7	1.0	23.7	21.1
Clethrionomys glareolus	–	–	15.8	2.8	3.2	0.2	2.3	0.4	10.5	8.0
Other rodents	1.4	1.9	–	–	–	–	–	–	–	–
Total rodents	25.9	5.1	15.8	2.8	10.5	1.5	7.0	1.4	34.2	29.1
Neomys fodiens	3.7	0.5	–	–	1.1	+	–	–	–	–
Sorex araneus	–	–	–	–	1.1	+	–	–	–	–
Sorex or *Neomys*	–	–	5.3	1.5	1.1	+	7.0	1.1	5.3	1.1
Talpa europaea	3.7	0.6	–	–	1.1	+	–	–	–	–
Total insectivores	7.4	1.1	5.3	1.5	4.2	0.2	7.0	1.1	5.3	1.0
Cervidae carcass	3.7	5.6	–	–	2.1	0.1	–	–	–	–
Birds	–	–	5.3	+	1.1	+	2.3	0.1	–	–
Rana temporaria	26.9	.	–	–	25.3	.	16.3	.	7.9	.
Rana arvalis	–	–	–	–	3.2	.	–	–	–	–
Rana spp.	25.9	.	36.8	.	25.3	.	39.5	.	6.3	.
Anura undetermined	33.3	.	57.9	.	51.6	.	39.5	.	52.6	.
Total anurans	81.5	87.9	94.7	95.4	93.7	98.1	90.7	97.4	65.8	69.9
Fish	7.4	0.3	5.3	0.3	–	–	2.3	+	–	–
Dytiscus spp.	–	–	–	–	9.5	0.1	2.3	+	–	–
Mean biomass consumed per 1 scat (g)	38.6		18.6		28.2		29.5		11.9	
Food niche breadth B	1.3		1.1		1.0		1.0		1.7	

moved in close proximity to water courses, which suggested searching for anurans. In dry forests, where water courses were scarce, the most common polecat foraging activity was hunting rodents, predominantly by digging for them (Tab. 3).

Discussion

Polecats have been classified as unspecialized predators (ERLINGE 1986) because most studies done in Europe, in many different habitats, including human settlements (review in BLANDFORD 1987), showed that polecats fed on rodents, birds, rabbits, rats, and eggs (KRATOCHVIL 1952; DANILOV and RUSAKOV 1969; RZEBIK-KOWALSKA 1972; BRUGGE 1977; WALTON 1977; HERRENSCHMIDT 1982; LODE 1990). In the pristine broadleaf forests of Białowieża National Park, polecats proved to be food and habitat specialists. They lived near running and stagnant waters and fed predominantly on anurans. This positive association between polecats and water was reported by DANILOV and RUSAKOV (1969), JENSEN and JENSEN (1972), and LODE (1988). Some previous studies showed the presence of amphibians in the polecat diet (KRATOCHVIL 1952; DANILOV and RUSAKOV 1969; RZEBIK-KOWALSKA 1972; BRUGGE 1977; WALTON 1977; LODE 1988, 1990), but only few proved amphibians to be the main prey (WEBER 1989 a, b), and none have documented that anurans comprise up to 98 % of biomass consumed by polecats as found in the present study.

In rich oldgrowth forests, the community of mammalian predators and raptors is composed of 23 species (JĘDRZEJEWSKI and JĘDRZEJEWSKA 1993). The polecat's niche (considering both habitat and food) as a semiaquatic predator is quite different from all other terrestrial predators (JĘDRZEJEWSKI et al. 1989). Its food niche is similar to that of the

Table 3. **Differentiated foraging activities of polecat in wet forests (bog alderwood and riverside ash-alder forest) and dry forests (oak-linden-hornbeam forest and spruce-pine forest) during snow period**

Data of snowtracking from the winters of 1986/87, 1987/88, and 1990/91. Total length of snowtracking in wet forests – 6775 m, in dry forests – 4195 m. Differences between habitats: * $p < 0.025$, $G = 5.21$, $df = 1$; *** $p < 0.001$, $G = 60.85$, $df = 1$ (G-test)

Activity	Number or length (m) per 1 km of trail	
	Bog alderwoods and riverside ash-alder forest	Oak-linden-hornbeam forest and spruce-pine forest
Foraging on stream[1]:		
– wading in water or walking on ice	11.1	2.6
– length of moving on ice	325.2 m	21.0 m
– looking under banks	10.0	1.7
Hunting rodents:		
– all attacks on rodents	4.9	14.8*
– attacks by digging	2.9	12.2
Intensity of area searching:		
– following own trail	51.5 m	9.3 m***

[1] differences in polecat foraging on stream in the two habitats were obviously the result of scarcity of water sources in dry forests.

river otter *Lutra lutra*. The otters, however, live on larger rivers in the Park (Narewka and Hwoźna) and do not inhabit small forest streams, the main polecat habitat (Brzeziński et al. 1993). The American mink *Mustela vison*, a newcomer to the community, may have a similar food and habitat niche as that of the polecat. However, the studies performed on mink in other parts of northeastern Poland showed that it is a generalistic predator, not specializing in anurans (Brzeziński and Zurowski 1992). In the Swiss mountain forest, rodents were more numerous than frogs, but frogs were eaten more frequently by polecats (Weber 1989b). In our study area, polecats extensively utilized forest rodents only in a year of high rodent numbers (1990) following a year of heavy mast production (acorn and hornbeam seeds).

Polecats are well adapted for capturing anurans. Weber (1989b), found on the basis of enclosure experiments, that frogs were more easily captured by polecats than were rodents. Polecats were able to locate and excavate frogs from 30 cm of soil, even when snow cover was up to 1 m thick. Polecats also eat toads (Weber 1989a; Lode 1990) which are inedible for most mammalian predators. In the temperate climates, common frogs *Rana temporaria* (the polecats' main prey) hibernate from the second half of October through early March (Juszczyk 1987). During mild winters, when the temperature is above 0 °C, frogs often become active (Savage 1961). Active frogs were observed at the Orłówka stream in January and February (personal observation). This species hibernates in the mud at the bottom of small water courses or under roots in the river banks (Savage 1961; Juszczyk 1987). Polecats are able to excavate frogs from the mud (Rzebik-Kowalska 1972; Lode 1988; Weber 1989b). High consumption of amphibians during winter can also be explained by the fact that polecats, like other small mustelids (see Jędrzejewska and Jędrzejewski 1989), store excess prey captured under favourable conditions and exploit the stores when conditions become too harsh for hunting. Rusakov (1962), Danilov and Rusakov (1969), and Lode (1989) found a few to several dozen dead animals (mainly frogs, rodents and birds) stored in polecat dens. Danilov and Rusakov (1969) reported that, during extremely cold periods, polecats did not leave their dens. This is possible if stored food supplies are utilized.

Preference for wet habitats and specialization in anurans have, however, one disadvantage in the temperate zone. In severe winters, streams and bogs freeze deeply, depriving polecats of anuran resources for prolonged periods. Under those conditions, polecats may abandon their well defined, nearly linear, territories along the stream (Brzeziński et al. 1992) and disperse over drier forest habitats, trying to survive by hunting rodents and scavenging. Many of them end up in human settlements. In the Białowieża Primeval Forest, the dry forests were utilized more during frosty weather, and in the village of Białowieża, highest numbers of polecats raiding domestic animals were captured by farmers in January and February, the coldest months of the year (Brzeziński et al. 1992).

In hunting rodents, polecats dig them up much the same as they dig for amphibians. Digging, effective even in winter, seems to be a general behaviour of the *Putorius* subgenus of mustelids; *Mustela putorius* digs for anurans and rodents, *M. eversmanni* digs up susliks *Citellus* spp. and other rodents (Kydyrbaev 1988), and *Mustela nigripes* digs up prairie dogs *Cynomys* spp. (Campbell et al. 1987; Richardson et al. 1987).

Observations reported here and results from other studies suggest the following generalisations:

1. In its pristine forest habitat, *Mustela putorius* is a specialized hunter for anurans and lives near small streams and bogs.
2. Regular seasonal freezing of water sources resulted in evolution of an alternate adaptation; under natural conditions this facultative "buffer" adaptation is hunting forest rodents (by digging them up) and by scavenging on ungulate carcasses.
3. In the man-made landscape, particularly with drainage and land reclamation projects that degraded polecat habitat throughout Europe, these predators had to rely on what used to be their facultative adaptation in order to survive.

Acknowledgements

We are grateful to the technical staff of the MRI for their assistance. E. Bujko, M. Swić, M. Szlachciuk, and K. Zub helped in the field work, N. Wojcieszuk, S. Bogdańska, and L. Szymura did the laboratory analysis and helped in computer data input. We appreciate the help of L. Siemieniuk with meteorological data. Drs D. Biggins, J. Goszczyński, and Z. Pucek kindly commented on the first draft. The study was supported by the grant CPBP 04.10 and partly by the Earthwatch grant.

Zusammenfassung

Selektive Nutzung des Lebensraumes im Winter durch Iltisse (Mustela putorius) und ihre Nahrung im Nationalpark Białowieża, Polen

Bevorzugte Lebensräume von Iltissen (*Mustela putorius*) wurden im Białowieża Nationalpark auf einer Fläche von 11,2 km^2 in 5 Wintern (1985/86–88/89 und 1990/91) über Häufigkeiten von Fährten im Schnee ermittelt. Danach waren Iltisse vornehmlich in feuchten Habitaten (am Fluß gelegene Erlen-Esche- und Erlenbruchwälder) anzutreffen. Trockene Regionen (Eiche-Linde-Hainbuche und Fichte-Kiefer-Einstände) wurden seltener aufgesucht. Die Intensität der Lebensraumnutzung änderte sich jedoch mit dem winterlichen Wetter. An relativ milden Tagen (0 bis −5 °C) wurden Iltisspuren doppelt so häufig in feuchten Waldungen gefunden wie in trockenen, bei Temperaturen zwischen −6 und −10 °C näherte sich dieses Verhältnis 1:1, und bei Temperaturen unter −10 °C, als die meisten fließenden und stehenden Gewässer gefroren waren, konnten in den trockenen Waldregionen doppelt so viele Iltisspuren festgestellt werden wie in den feuchten. Nahrungsanalysen an 222 Kotproben von Iltissen aus 5 Wintern (1986/87–1990/91) ergaben, daß Anuren (hauptsächlich *Rana temporaria*) in 60–95 % der Kotproben 70–98 % der Biomasse ausmachten. Auf Nagetiere (hauptsächlich *Apodemus flavicollis* und *Clethrionomys glareolus*) entfielen nur 1–29 % der konsumierten Biomasse. Der Nagetieranteil nahm mit abnehmender Wintertemperatur zu, aber auch mit zunehmender Abundanz der Nager. Verfolgungen von Spuren einzelner Individuen zeigte, daß sich die Tiere in den feuchten Waldregionen in der Nähe der Gewässer bewegten und Anuren suchten. In den trockenen Standorten erbeuteten sie Nagetiere hauptsächlich durch Ausgraben.

References

Blandford, P. R. S. (1987): Biology of the polecat *Mustela putorius:* a literature review. Mammal Rev. **17**, 155–198.

Brugge, T. (1977): Prey selection of weasel, stoat and polecat in relation to sex and size. Lutra **19**, 39–49.

Brzeziński, M.; Zurowski, W. (1992): Spring diet of the American mink *Mustela vison* in the Mazurian and Brodnica Lakelands, northern Poland. Acta theriol. **37**, 193–198.

Brzeziński, M.; Jędrzejewski, W.; Jędrzejewska, B. (1992): Winter home ranges and movements of polecats *Mustela putorius* in Białowieża Primeval Forest. Acta theriol. **37**, 181–191.

Brzeziński, M.; Jędrzejewski, W.; Jędrzejewska, B. (1993): Diet of otters *Lutra lutra* inhabiting small rivers in the Białowieża National Park, eastern Poland. J. Zool. (Lond.) (in press).

Campbell, T. M., III; Clark, T. W.; Richardson, L.; Forrest, S. C.; Houston, B. R. (1987): Food habits of Wyoming black-footed ferrets. Amer. Midl. Nat. **117**, 208–210.

Danilov, P. I.; Rusakov, O. S. (1969): Peculiarities of the ecology of *Mustela putorius* in north-west districts of the European part of the USSR. Zool. Zhurn. **48**, 1383–1394.

Debrot, S. (1982): Atlas des poils de mammifères d'Europe. Université de Neuchâtel.

Erlinge, S. (1986): Specialists and generalists among the mustelids. Lutra **29**, 5–11.

Fairley, J. S.; Ward, D. P.; Smal, C. M. (1987): Correction factors and mink faeces. Ir. Nat. J. **22**, 334–336.

Faliński, J. B. (1986): Vegetation dynamics in temperate lowland primeval forest. Geobotany **8**, 1–537.

Herrenschmidt, V. (1982): Note sur les déplacements et le rythme d'activité d'un Putois *Mustela putorius* suivi par radiotracking. Mammalia **46**, 554–556.

Jensen, A.; Jensen, B. (1972): Ilderen (*Putorius putorius*) og Ilderjadten i Danmark 1969/70. Danske Vildundersøgelser **18**, 1–32.

Jędrzejewska, B.; Jędrzejewski, W. (1989): Seasonal surplus killing as hunting strategy of the weasel *Mustela nivalis* – test of a hypothesis. Acta theriol. **34**, 347–359.

Jędrzejewski, W.; Jędrzejewska, B. (1992): Foraging and diet of the red fox *Vulpes vulpes* in relation to variable food resources in Białowieża National Park, Poland. Ecography **15**, 213–221.

Jędrzejewski, W.; Jędrzejewska, B. (1993): Predation on rodents in Białowieża Primeval Forest, Poland. Ecography **16** (in press).

Jędrzejewski, W.; Jędrzejewska, B.; Szymura, A. (1989): Food niche overlaps in a winter community of predators in the Białowieża Primeval Forest, Poland. Acta theriol. **34**, 487–496.

Juszczyk, W. (1987): Płazy i gady krajowe. [Amphibians and reptiles of the country]. 2nd ed. Vol. 2. Warszawa: PWN – Polish Scientific Publishers.

Kratochvil, J. (1952): O potrave a rasach tchore tmaveho (*Putorius putorius* L.). Acta Univ. Agric. Silv. Brno **1**, 43–60.

Kydyrbaev, H. K. (1988): Ekologiya svetlogo horka v Kazakhstane. [Ecology of the steppe polecat in Kazakhstan]. In: The ecology and behaviour of mammals in Kazakhstan. Alma-Ata: Academy of Sciences of the Kazakh SSR, 56–68.

Levins, R. (1968): Evolution in changing environments. Princeton, N. Y.: Princeton Univ. Press.

Lockie, J. (1959): The estimation of the food of foxes. J. Wildl. Manage. **23**, 224–227.

— (1961): The food of the pine marten *Martes martes* in West Ross-Shire, Scotland. Proc. zool. Soc. Lond. **136**, 187–195.

Lode, T. (1988): Note preliminaire sur la biologie du comportement du Putois *Mustela putorius* L. dans les bocages humiges de l'Ouest de la France. Bull. Soc. Sci. Nat. Ouest France, Museum Nantes **10**, 58–67.

— (1989): Le comportement de mise en réserve alimentaire des proies chez le putois *Mustela putorius.* Cahiers Ethol. Appl. **9**, 19–30.

— (1990): Le régime alimentaire d'un petit carnivore, le putois *Mustela putorius* dans l'ouest de la France. Gibier Faune Sauv. **7**, 193–203.

März, R. (1987): Gewöll- und Rupfungskunde. Berlin: Akademie-Verlag.

Mermod, C.; Debrot, S.; Marchesi, P.; Weber, J.-M. (1983): Le putois *Mustela putorius* L. en Suisse romande. Rev. suisse Zool. **90**, 847–856.

Olszewski, J. L. (1986): The role of forest ecosystems in modifying local climate of the Białowieża Primeval Forest, as revealed by air temperature characteristics. Wroclaw: Wyd. PAN (Prace habilitacyjne), Ossolineum.

Pucek, Z. (1981): Keys to vertebrates of Poland. Mammals. Warszawa: PWN – Polish Scientific Publishers.

Richardson, L.; Clark, T. W.; Forrest, S. C.; Campbell, T. M. III, (1987): Winter ecology of black-footed ferrets (*Mustela nigripes*) at Meeteetse, Wyoming. Amer. Midl. Nat. **117**, 225–239.

Roger, M.; Pascal, M.; Pruniere, P. (1991): Facteurs correctifs de quantification du régime alimentaire du putois *Mustela putorius* L. Gibier Faune Sauv. **7**, 343–357.

Rzebik-Kowalska, B. (1972): Studies on the diet of the carnivores in Poland. Acta zool. crac. **17**, 415–506.

Rusakov, O. S. (1962): Some data on the nutrition of the European polecat in Leningrad, Pskov and Novgorod oblast. Sb. Nauch. Statei Zapadnogo Otd. Vsesoyuznogo Nauchno-Issled. Inst. Zhivotnogo Syrya Pushniny **2**, 195–199.

Savage, R. (1961): The ecology and life history of the common frog *Rana temporaria*. London: Pitman.

Schaff, E. (1911): Die wildlebenden Säugetiere Deutschlands. Neudamm.

Walton, K. C. (1977): Polecat. In: The Handbook of British Mammals. Ed. by G. B. Corbet and H. N. Southern. 2nd ed. Oxford: Blackwell Sci. Publ. 345–352.

Weber, D. (1989a): Foraging in the polecats *Mustela putorius* L. in Switzerland: The case of a specialist anuran predator. Z. Säugetierkunde **54**, 377–392.

— (1989b): The diet of polecats (*Mustela putorius*) in Switzerland. Z. Säugetierkunde **54**, 157–171.

Authors' addresses: Włodzimierz Jędrzejewski, Mammal Research Institute, Polish Academy of Sciences, PL-17-230 Białowieża; Bogumiła Jędrzejewska, Workshop for Ecology and Protection of the Natural Environment, P.O. Box 23, PL-17-230 Białowieża; Marcin Brzeziński, Department of Ecology, University of Warsaw, Krakowskie Przedmieście 26/28, PL-00-927 Warsaw, Poland

Z. Säugetierkunde 58 (1993) 84–91

ISSN 0044-3468

Effectifs et activités du chat domestique (*Felis catus*) dans le Jura suisse

Par NICOLE LACHAT, S. AUBRY, N. FERRARI, J. S. MEIA, C. MERMOD et J. M. WEBER

Institut de Zoologie, Université de Neuchâtel, Neuchâtel, Suisse

Réception du Ms. 26. 3. 1992
Acceptation du Ms. 28. 9. 1992

Abstract

Number and activities of farm cat (Felis catus) in the Swiss Jura

Investigated a domestic farm cat (*Felis catus*) population in the Swiss Jura by nightlighting and daily counts. 172 counts were done (107 at night-, 65 at daytime). 2060 cats were observed, their behaviour and the habitat they used noted. The most frequent activity is hunting (47.1 %). Cat number fluctuates according to months. Weather influence is important.

Introduction

Dans le cadre d'une étude globale des prédateurs du campagnol terrestre (*Arvicola terrestris scherman*), une population de chats de ferme a été suivie régulièrement durant 3 ans, de juillet 1988 à juin 1991. Les activités, les milieux fréquentés et les interactions avec d'autres espèces ont été relevés. La majorité des observations se sont faites par la technique du phare, technique utilisée depuis de nombreuses années par une grande quantité de biologistes de terrain de tous les pays. Cette méthode est efficace pour recenser une grande variété d'espèces, depuis le lièvre (SALZMANN et SALZMANN 1973) jusqu'au cerf (PROGULSKE et DUERRE 1964), en passant par le renard (ROBOLY 1985; WEBER et al. 1991).

Nous avons effectué des parcours au phare pour étudier les chats durant la nuit et nous avons parcouru les mêmes parcours de jour, de manière à avoir un aperçu complet de leurs activités.

Matériel et méthodes

L'étude est réalisée dans le Jura suisse (N-W du canton de Berne), à la frontière avec les cantons de Neuchâtel et du Jura (47° 09′ N, 6° 56′ E).

Il s'agit d'une zone de 30 km^2 dont l'altitude varie entre 900 et 1290 mètres.

Ce terrain de La Chaux d'Abel présente une topographie vallonnée, le paysage étant divisé par plusieurs lignes de crêtes aux versants boisés souvent abrupts.

La principale activité humaine est l'élevage des bovins. Des fermes (environ 80) sont réparties sur toute la surface et reliées entre elles par de nombreuses petites routes.

La région se présente sous la forme d'une mosaïque de prairies (23 %), de pâturages (57 %), boisés ou non et de forêts (20 %) où l'épicéa (*Picea abies*) domine.

Le climat est humide, les saisons contrastées. L'hiver peut être très rigoureux, la température descendant régulièrement au-dessous de 0°, parfois jusqu'à −30° en janvier et février.

Une enquête par questionnaires dans les fermes a permis d'estimer à 600 individus la population de chats du terrain d'étude.

La méthode a été décrite par WEBER et al. (1991). Dans notre cas, les tournées sont effectuées chaque mois, selon le plan suivant:
3 nuits consécutives: de 21 h à minuit (A), de minuit à 3 h (B), de 3 h à 6 h (C);
1 tournée le matin (D);
1 tournée l'après-midi (E).

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5802-0084 $ 02.50/0

Tous les chats sont recensés, hormis ceux situés à proximité immédiate des habitations. Ceux-ci n'étaient pas éclairés pour éviter de déranger les habitants. Chaque fois que cela est possible, le comportement du chat est relevé, de même que le type de milieu dans lequel évolue l'animal.

Six types d'activités sont retenus : affût et chasse, déplacement, toilettage, repos, fuite, interaction inter- ou intra-spécifique.

Sept types de milieux sont distingués : pâturage; prairie cultivée; forêt; lisière, bouquet d'arbres ou haie; champ labouré; chemin ou route; mur de pierres sèches.

Résultats

172 tournées (107 nocturnes, 65 diurnes) ont eu lieu. Ceci représente un total de 2060 observations (Tab. 1). Le nombre de chats observés n'est pas significativement différent entre les périodes de relevés (A, B, C, D, E) (test Kruskall-Wallis 1-way Anova, khi^2 =

Tableau 1. **Nombre de chats vus chaque mois**
A, B, C, D, E correspondent aux différentes tournées

Mois/Année	A	B	C	D	E	Total
7/88	26	13	–	8	15	62
8/88	39	11	26	16	22	114
9/88	32	16	17	16	10	91
10/88	30	32	10	15	23	110
11/88	7	9	3	0	0	19
12/88	2	0	1	0	1	4
1/89	0	1	1	5	1	8
2/89	12	4	2	6	9	33
3/89	19	14	22	19	9	83
4/89	10	5	16	13	9	53
5/89	18	21	10	18	4	71
6/89	28	29	18	3	17	95
7/89	29	18	22	8	5	82
8/89	8	21	19	9	10	67
9/89	16	33	12	–	–	61
10/89	7	15	12	10	31	75
11/89	28	12	15	22	28	105
12/89	21	14	17	–	–	52
1/90	22	13	2	4	–	41
2/90	17	11	7	–	–	35
3/90	19	13	11	13	15	71
4/90	4	10	19	21	18	72
5/90	13	9	14	8	11	55
6/90	11	8	28	1	8	56
7/90	31	18	26	12	14	101
8/90	8	26	5	7	18	64
9/90	16	7	4	10	19	56
10/90	8	7	22	20	0	57
11/90	12	15	3	0	16	46
12/90	0	0	0	0	0	0
1/91	0	0	0	0	0	0
2/91	0	2	2	1	2	7
3/91	8	5	10	21	21	65
4/91	1	4	4	0	2	11
5/91	10	4	11	18	13	56
6/91	26	18	29	5	4	82
Total	538	438	420	309	355	2060
m	14.9	12.2	12	9.4	11.1	
%	26.1	21.3	20.4	15	17.2	

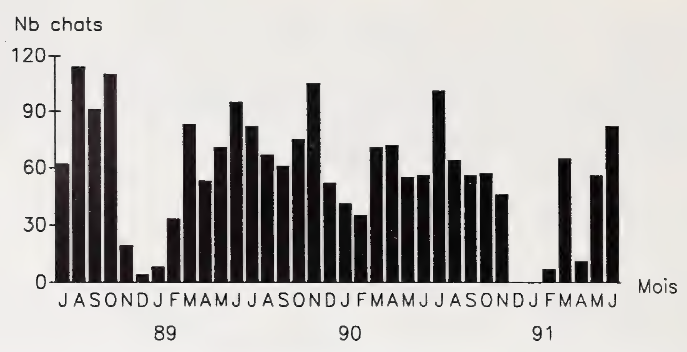


Fig. 1. Fluctuations des observations de chats, toutes tournées confondues. Nb – nombre

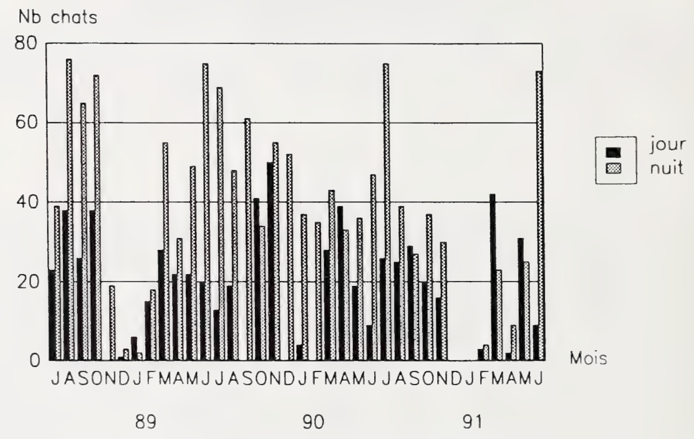


Fig. 2. Fluctuations des observations de chats durant les tournées de jour et de nuit. Nb – nombre

2.45, p = 0.6). La répartition des observations entre le jour et la nuit n'est pas significativement différente (test U de Mann-Whitney, p = 0.19), bien que le nombre moyen de chats observés par tournée soit légèrement plus élevé durant la nuit (13 individus) que durant le jour (10.3).

La quantité d'observations fluctue de manière hautement significative avec les mois (test Kruskall-Wallis, $khi^2 = 51.36$, $p < 0.0001$) (Fig. 1). Elle diminue chaque hiver, aussi bien pour les tournées diurnes que nocturnes. Durant l'hiver 89/90 qui fut particulièrement clément et dépourvu de neige, la baisse s'avéra moindre (Fig. 2).

Les tournées de jour montrent que le nombre de chats diminue également durant les mois d'été, lorsque la température est par trop élevée. La nuit tombée et la fraîcheur revenue, les chats repartent en chasse.

La météo a une forte influence. Le mauvais temps retient significativement les chats à l'intérieur ou à proximité immédiate des habitations (test Kruskall-Wallis, $khi^2 = 57.52$, $p < 0.0001$) (Tab. 2).

Le comportement de 2039 chats a été relevé. Le type d'activité le plus fréquemment observé est «l'affût/chasse» (961/2039) (Tab. 3).

Des déplacements sont également régulièrement observés (624/2039), de même que des périodes de repos (405). L'activité de toilettage (19) et la fuite (8) ne sont que rarement observés.

Tableau 2. **Données météorologiques**
A, B, C, D, E correspondent aux différentes tournées

Mois/Année	A	B	C	D	E
7/88	3	3	–	2	2
8/88	1	1	1	1	2
9/88	1	2	1	1	1
10/88	3	3	3	1	1
11/88	1	1	1	4	4
12/88	1[a]	1	2	4	4
1/89	1	1	1	1	1
2/89	4	4	1	3	3
3/89	1	1	2	1	1
4/89	4	3	4	3	4
5/89	1	1	1	1	1
6/89	1	1	1	3	3
7/89	1	1	2	3	1
8/89	1	1	1	1	3
9/89	1	1	1	–	–
10/89	1	1	1	3	2
11/89	1	2	1	1	1
12/89	1	3	2	–	–
1/90	1	1	3	4	–
2/90	1	1	1	–	–
3/90	1	1	2	1	1
4/90	3	2[a]	2	1	1
5/90	2	1	1	1	1
6/90	1	1	3	3	1
7/90	1	1	1	1	2
8/90	1	1	1	1	1
9/90	1	1	1	1	2
10/90	1	1	3	2	2
11/90	3	3	3[a]	1[a]	2
12/90	1[a]	1[a]	1[a]	1[a]	1[a]
1/91	4[a]	4[a]	4[a]	1[a]	1[a]
2/91	1[a]	1[a]	1[a]	1[a]	1[a]
3/91	4	3	4	1	1
4/91	1[a]	1[a]	1[a]	1[a]	2[a]
5/91	2	1	1	1	1
6/91	1	2	1	1	1

1 = beau, 2 = couvert, 3 = pluie, 4 = chutes de neige, [a]couverture neigeuse.

Tableau 3. **Types d'activité relevés durant les tournées**
A, B, C, D, E correspondent aux différentes tournées

	A	B	C	D	E	Total	%
Affût/chasse	250	199	175	155	182	961	47.1
Déplacement	174	120	117	95	118	624	30.6
Toilettage	3	3	2	7	4	19	0.9
Repos	99	105	110	45	46	405	19.9
Fuite	0	4	4	0	0	8	0.4
Interactions	7	5	2	6	2	22	1.1
Total	533	436	410	308	352	2039	100

Les interactions (22) concernent la plupart du temps des contacts intraspécifiques, mais d'autres espèces sont parfois concernées (renard *Vulpes vulpes*, fouine *Martes foina*, moyen-duc *Asio otus*) (Fig. 3).

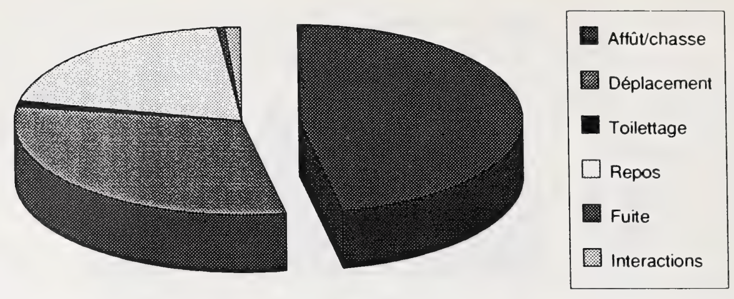


Fig. 3. Fréquence d'appariation (%) des différents types d'activité, toutes tournées confondues

Tableau 4. **Milieux fréquentés par les chats**

Pré, champ	1188	58.6 %
Pâturage	484	23.9
Chemin, route	177	8.7
Mur de pierres sèches	120	5.9
Lisière, bouquet d'arbres, haies	37	1.8
Champ labouré	17	0.9
Forêt	3	0.2
Total	2026	100

Les milieux fréquentés par les divers chats observés ont pu être identifiés dans 2026 cas. L'utilisation de ces milieux est très irrégulière (Tab. 4). Les plus visités sont les prés et les champs (1188/2026) où les chats vont chasser. Les pâturages sont également fréquemment utilisés, bien qu'en moindre mesure (484), malgré une surface plus importante sur notre terrain.

Les chemins et les routes sont régulièrement empruntés (177), notamment en hiver, ce qui facilite les déplacements d'un milieu à un autre.

Les murs de pierres sèches servent également pour les déplacements mais aussi et surtout pour des périodes de repos ou d'affût (120).

Les lisières, bouquets d'arbres ou haies sont exploités dans une moindre mesure (37). Les chats chassent de temps à autre dans les champs fraîchement labourés mais ne semblent pas trop les apprécier.

Finalement, des observations en forêt n'ont eu lieu qu'à 3 reprises. Il s'agissait à chaque fois d'animaux en déplacement.

Discussion

Le nombre de biologistes pratiquant l'observation au phare et la variété d'espèces étudiées par ce moyen attestent de l'utilité et de la valeur de cette technique dans l'étude d'une population animale.

Elle permet entre autres de suivre l'évolution d'une population sur un terrain défini, d'observer d'éventuelles fluctuations, saisonnières ou à long terme (Lord 1961; Eltringham et Flux 1971; Weber et al. 1991) mais aussi, comme dans notre cas, de récolter des informations sur le comportement nocturne des animaux. A l'encontre de certains auteurs (Lord 1959; Progulske et Duerre 1964), nous n'avons pas observé d'influence de la période d'observation sur les comptages. La répartition des observations est homogène entre les différentes tournées. Les chats sont actifs à n'importe quel moment de la nuit ou

du jour. Toutefois, il semble qu'ils manifestent une certaine préférence, sans que celle-ci soit significative, pour les activités nocturnes.

Ceci va à l'encontre des observations d'autres auteurs qui ont mis en évidence un schéma d'activité plutôt diurne, avec deux pics, à l'aube et au crépuscule (PANAMAN 1981).

On pourrait expliquer cette absence de pics d'activité par le fait que les chats reçoivent du lait à la ferme, le matin et le soir, au moment de la traite. Ces repas sont probablement suivis d'une période de repos.

Les variations saisonnières sont très importantes. Elles sont en étroite relation avec les conditions météorologiques.

La plupart des auteurs s'accordent généralement sur le rôle joué par la météo dans ce type de recensement, bien que cette influence soit variable selon les espèces (PROGULSKE et DUERRE 1964; FAFARMAN et WHYTE 1979; SALZMANN et SALZMANN 1973).

Dans le cas des chats, les observations diminuent considérablement en hiver, de jour comme de nuit, la neige jouant un rôle primordial dans l'intensité des activités. Nous en voulons pour preuve l'hiver 89/90 durant lequel la couverture neigeuse n'excéda pas quelques centimètres, et encore sur de courtes périodes. Les observations diminuèrent malgré tout durant ces mois, mais significativement moins que durant un véritable hiver comme celui de 90/91 ($khi^2 = 16.34$, $p < 0.001$). Cet hiver-là, nous ne fîmes aucune observation de chats pendant les mois de décembre et de janvier et les effectifs restèrent faibles jusqu'à fin avril, la reprise de mars 91 n'étant due qu'à une précoce tentative du printemps.

En ce qui concerne les mois d'été (juin à août), le nombre d'observations diurnes diminue également. Les chats n'apprécient pas les températures trop élevées. Par contre, durant les tournées de nuit, nous observons alors un nombre considérable de chats en activité.

Il apparaît donc que de mauvaises conditions météorologiques (chutes de neige, couverture neigeuse, pluie), de même que des températures extrêmes jouent un rôle déterminant dans le schéma d'activité des chats. Ceci est confirmé par d'autres auteurs: LAUNDRÉ (1977) montre qu'une météo défavorable diminue le temps que les chats passent à l' extérieur, loin des bâtiments. IZAWA (1983) relève l'influence de la température et de la pluie sur des chats harets.

La fréquence d'apparition de certaines activités est significativement différente selon les tournées considérées.

Les chats chassent de jour et de nuit mais les observations de bêtes à l'affût sont plus fréquentes la nuit, probablement à cause du moindre dérangement. En effet, le jour, l'activité humaine est importante sur notre terrain (travaux dans les champs). On assiste par conséquent également à plus de déplacements nocturnes. De même, le nombre de chats au repos entre deux périodes de chasse est aussi plus élevé la nuit que le jour.

Les contacts intraspécifiques interviennent de jour comme de nuit mais les interactions avec d'autres espèces se produisent la nuit essentiellement.

La plupart des chats ont été observés en milieux ouverts, particulièrement dans les prés et les champs. Ces zones étaient très riches en proies durant ces années. On y a recensé en effet entre 700 et 1000 campagnols terrestres par hectare (WEBER et AUBRY 1991). Les pâturages sont moins utilisés, sans doute en raison d'une plus petite densité de proies mais aussi peut-être à cause de la présence du bétail.

Les chats utilisent régulièrement les murs de pierres sèches. Les arbustes et les buissons présents le long de ces murs leur permettent de passer inaperçus lors de leurs déplacements, de se camoufler pour guetter les oiseaux ou pour se reposer. De plus, ces murs sont des passages à sec lorsque le terrain est détrempé par la pluie.

Finalement, la diminution des observations durant la période d'étude ne devrait pas indiquer une réelle baisse de la population de chats. La chute des populations de campagnols terrestres lors des derniers mois du recensement a sans doute provoqué une

réorientation de la stratégie alimentaire des chats, les amenant à se nourrir d'autres aliments et à dépendre à nouveau plus étroitement du nourrissage par les paysans et des ressources exploitables dans ou aux alentours des fermes (Sen Gupta, comm. pers.).

Remerciements

Nous tenons à remercier les habitants de notre terrain d'étude pour leur compréhension ainsi que M. alfred Hennet, garde-faune, pour sa collaboration.

Nous sommes reconnaissants envers Mme Jacqueline Moret pour ses conseils en statistiques.

Cette étude a été financée en partie par l'Office Fédéral de l'Environnement, des Forêts et du Paysage et par les Départements de l'Agriculture de 16 Cantons.

Résumé

Une population de chats du Jura suisse a été suivie de juillet 1988 à juin 1991. La technique du phare ainsi que des comptages diurnes ont été utilisés.

Les tournées ont eu lieu chaque mois, une fois le matin, une fois l'après-midi ainsi que trois nuits consécutivement.

172 tournées furent effectuées (107 nocturnes et 65 diurnes) permettant l'observation de 2060 chats, de leurs activités et des milieux fréquentés. L'activité la plus fréquemment relevée est la chasse (47.1 %).

Le nombre de chats fluctue avec les mois. Il diminue en hiver et durant les mois d'été. L'influence de la météo est importante.

Zusammenfassung

Bestand und Verhalten der Hauskatze (Felis catus) im Schweizer Jura

Eine Katzenpopulation (*Felis catus*) im Schweizer Jura wurde von Juli 1988 bis Juni 1991 mittels Scheinwerfer und täglichen Zählungen untersucht.

Probezählungen erfolgten monatlich, und zwar jeweils morgens, abends und in den drei folgenden Nächten.

Die 172 durchgeführten Probezählungen (107 nachts, 65 am Tage) ermöglichten Beobachtungen von 2060 Katzen, im Hinblick auf ihr Verhalten und die genutzten Biotope.

Das am häufigsten beobachtete Verhalten war die Jagd (47,1 %). Die Anzahl der Katzen wechselte im Verlauf des Jahres. Sie nahm im Winter und während der Sommermonate ab. Der Einfluß des Wetters war bedeutend.

Références

Eltringham, S. K.; Flux, J. E. C. (1971): Night counts of hares and other animals in East Africa. E. Afr. Wildl. J. **9**, 67–72.

Fafarman, K. R.; Whyte, R. J. (1979): Factors influencing nighttime roadside counts of cottontail rabbits. J. Wildl. Manage. **43**, 765–767.

Izawa, M. (1983): Daily activities of the feral cat *Felis catus* Linn. J. Mammal. Soc. Japan **9**, 219–228.

Laundre, J. (1977): The daytime behaviour of domestic cats in a free-roaming population. Anim. Behav. **25**, 990–998.

Lord, R. D., Jr. (1959): Comparison of early morning and spotlight roadside censuses for cottontails. J. Wildl. Manage. **23**, 458–460.

Lord, R. D., Jr. (161): Seasonal changes in roadside activity of cottontails. J. Wildl. Manage. **25**, 206–209.

Panaman, R. (1981): Behaviour and ecology of free-ranging female farm cat. Z. Tierpsychol. **52**, 59–73.

Progulske, D. R.; Duerre, D. C. (1964): Factors influencing spotlighting counts of deer. J. Wildl. Manage. **28**, 27–34.

Roboly, O. (1985): Etude des populations de certains canidés sauvages ou errants à l'occasion du tir de nuit. Rev. Ecol. (Terre Vie) **40**, 187–188.

Salzmann, I.; Salzmann, H. C. (1973): Erste Erfahrungen bei Feldhasenzählungen mit Scheinwerfern. Jb. Naturhist. Mus. Bern **5**, 201–216.

Weber, J. M.; Aubry, S. (1991): Red fox predation on the fossorial form of the water vole, in western Switzerland. XXth UIGB-Congress, 21–26 August 1991, Gödöllö, Hungary.

Weber, J. M.; Aubry, S.; Lachat, N.; Meia, J. S.; Mermod, C.; Paratte, A. (1991): Fluctuations and behaviour of foxes determinated by nightlighting: preliminary results. Acta Theriol. **36**, 285–291.

Adresse des auteurs: Nicole Lachat, Stéphane Aubry, Nicola Ferrari, Jean-Steve Meia, Claude Mermod, Jean-Marc Weber, Institut de Zoologie, Université de Neuchâtel, Chantemerle 22, CH-2007 Neuchâtel, Suisse

Z. Säugetierkunde 58 (1993) 92–115

ISSN 0044-3468

Die Schmelzmuster in den Schneidezähnen der Gliroidea (Gliridae und Seleviniidae, Rodentia, Mammalia) und ihre systematische Bedeutung[1]

Von W. v. Koenigswald

Institut für Paläontologie der Universität Bonn, Deutschland

Eingang des Ms. 22. 4. 1992
Annahme des Ms. 6. 7. 1992

Abstract

The schmelzmuster of the incisors in Gliroidea (Gliridae and Seleviniidae, Rodentia, Mammalia) and their systematic significance

Investigated is the enamel ultrastructure in incisors of about 20 fossil and extant gliroid genera and subgenera. According to the schmelzmuster of the lower incisor three groups can clearly be differentiated. Group 1 contains *Myoxus* and *Glirulus* having mainly transversly orientated Hunter-Schreger bands (HSB) and a thick prismless external enamel (PLEX). The schmelzmuster of group 2 is more derived in having diagonally orientated HSB. This group contains *Dryomys, Eliomys* with its several fossil subgenera from the Mediterranean islands, and *Leithia, Microdyromys,* and *"Peridyromys" brailloni.* Group 3 with the most derived schmelzmuster characterized by longitudinally arranged HSB covers *Graphiurus, Myomimus, Miodyromys, Muscardinus, Selevinia,* and *Plioselevinia.* This schmelzmuster is represented at least since the early Middle Miocene (MN 4) and indicates the early separation of these groups. This allows plenty of time for further differentiation in other characters. The probability of parallelism has to be rejected according to a survey of other rodents with rearranged HSB. Group 3 is tying together the Seleviniidae with some but not all Gliridae. Therefore, the Seleviniidae are not a sister group of the Gliridae in general and should be incorporated into the Gliridae. The grouping according to the schmelzmuster contradicts to some degree the systematic arrangement according to molar morphology (Daams 1981) but corresponds widely with the analysis of soft parts as done by Kratochvil (1973). This indicates the importance of the enamel analysis.

Einleitung

Die Schneidezähne der Nagetiere sind in ihrer äußeren Morphologie recht arm an Merkmalen. Der Zahnschmelz aber, der als dünne Auflage die labiale Seite der Schneidezähne bedeckt, bietet ein bisher oft nur ungenügend genutztes Informationspotential, das aber für systematische Fragestellungen zusätzlich zur Morphologie (Thenius 1989) sehr bedeutsam sein kann.

Die klassischen Unterordnungen der Rodentia lassen sich in gewissem Maße am Schmelz der Schneidezähne unterscheiden (Korvenkontio 1934; Boyde 1978). Auch innerhalb der Unterordnungen zeichnen sich systematisch relevante Gruppen ab. So konnte Martin (1992) innerhalb der Caviomorpha und Hystricognatha neue Argumente für die phylogenetischen Beziehungen am Schmelz der Schneidezähne aufzeigen. Stellenweise lassen sich sogar einzelne Familien (z. B. Eomyidae, Wahlert und Koenigswald 1985) oder Gattungen (z. B. *Marmota,* Koenigswald 1990) durch Besonderheiten im Schmelzmuster kennzeichnen.

[1] Diese Studie möchte ich meinem Kollegen und Freund, Herrn Prof. Dr. Jochen Niethamer, Bonn, in Dankbarkeit widmen, der in der Säugetierkunde die Zoologen und Paläontologen zusammenhielt und stets bereit war, mit Rat und Material zu helfen. Seit einem schweren Unfall auf der Sommerexkursion 1991 kann er am wissenschaftlichen Leben nicht mehr teilhaben.

Für die Gliriden beschreibt bereits Korvenkontio (1934) Unterschiede im Inzisivenschmelz. Die hier vorgelegte Studie zeigt, daß die Gliroidea (Gliridae und Seleviniidae) unter Einschluß des Fossilmaterials aufgrund der Schmelzanalyse in drei Gruppen aufgeteilt werden können. Die zunehmende Abwandlung von einem Grundmuster läßt sich als phylogenetische Entwicklung deuten. Dieser Merkmalskomplex ist für die Systematik der fossilen und rezenten Gliroidea von großer Bedeutung, weil die bisherigen Gliederungen, die sich im wesentlichen nur auf die Morphologie der Molaren stützen konnten, zu recht widersprüchlichen Hypothesen gekommen sind.

Da der Zahnschmelz fossiler Säugetiere meist nur geringe diagenetische Veränderungen aufweist, können bei der Schmelzanalyse fossile und rezente Gattungen nach gleicher Methode untersucht werden. Allerdings liegen von wenigen fossilen Gattungen die Inzisiven vor, weil fossile Kleinsäuger in der Regel durch Schlämmen aus großen Sedimentmengen geborgen werden, und dabei geht häufig der Zusammenhang von Schneidezähnen und Backenzähnen verloren.

Anlaß für diese Studie war die Gelegenheit, erstmalig das Schmelzmuster der Schneidezähne vom seltenen kasachischen Salzbilch, *Selevinia betbakdalaensis,* zu analysieren und an dem bislang nicht genutzten Merkmalskomplex die Beziehung mit den Gliridae zu überprüfen. Dafür ist ein möglichst umfassender Vergleich innerhalb der Gliroidea notwendig.

Material und Methoden

Der Gattungname *Glis* Brisson, 1762 ist nach Honacki et al. (1982) nicht gültig. Statt dessen ist der Gattungname *Myoxus* Zimmermann, 1780 zu verwenden. Dies hätte auch formale Konsequenzen für die höheren Kategorien wie Gliridae und Gliroidea, die aber hier zunächst beibehalten werden.

Zähne folgender Taxa standen für die Analyse zur Verfügung:

Rezente Gliridae

Dryomys nitedula (Pallas, 1778), Kleinalm, Niedere Tauern, Österreich, [KOE 923 ex Slg. Niethammer 1227]
Dryomys nitedula (Pallas, 1778), Jugoslawien, [KOE 1504 ex SMF 19791]
Eliomys guercinus (L., 1766), [KOE 961 ex Slg. J. Niethammer]
Eliomys quercinus (L., 1766), Trier/Mosel, [KOE 966 ex Slg. J. Niethammer]
Myoxus glis (L., 1766), Tübingen, [KOE 35]
Glirulus japonicus (Schinz, 1845), Japan, [KOE 1500, Shusaku Minato ded]
Graphiurus murinus (Desmarest, 1822), Kanyawara, [KOE 1536 ex SMNS 26323]
Graphiurus sp., Rietfontein/Windhoek, [KOE 963 ex Slg. J. Niethammer]
Muscardinus avellanarius (L., 1758), [KOE 962 ex Slg. J. Niethammer]
Muscardinus avellanarius (L., 1758), Mosel, [KOE 965 Slg. J. Niethammer]
Myomimus roachi (Bate, 1937), Endirne/Türkei, [KOE 1503 ex SMF 77286]

Fossile Gliridae

Anthracoglis marinoi Engesser, 1983, Ober-Miozän, Bacinello VI, [KOE 1557 det. B. Engesser es NHMB]
Eliomys (Hypnomys) sp., Jungpleistozän oder Holozän, Pen Majol (Mallorca), [KOE 1002, det. H. de Bruijn]
Eliomys (Maltamys) gollcheri (Bruijn, 1966), Pleistozän, Mnaidra Gap, Matlta, [KOE 999 det. H. de Bruijn]
Eliomys (Maltamys) wiedincitensis Zammit Maempel und Bruijn, 1982, Pleistozän (Leithia-castei-Stufe), Ghar-Dalam-Höhle, Malta, [KOE 1505 leg. G. Storch 1970]
Eliomys (Tyrrhenoglis) majori Engesser, 1976, Ober-Pliozän, Capo Figari (Sardinien), [KOE 1559 det. B. Engesser ex NHMB]
Leithia melitensis (Adams, 1863), Pleistozän, Mnaidra Gap, Malta, [KOE 1506 leg. G. Storch ex SMF]

Microdyromys miocaenicus Baudelot, 1965, Mittel-Miozän (MN 6), Sansan, [KOE 1558 det. B. Engesser ex NHMB]
Miodyromys aegercii Baudelot, 1972, Mittel-Miozän (MN 6), Steinberg/Nördlinger Ries, [KOE 995, 1560 ex BSPM 1970 XVIII]
Miodyromys biradiculus Mayr, 1979, Mittelmiozän (MN4), Petersbuch 2, Fränkische Alb, [KOE 1550, 1563 ex BSPM]
Myomimus roachi (Bate, 1937), Jungpleistozän, Hayonim Cave, Layer B, Israel, [KOE 1538, det. E. Tchernov]
Myomimus gafzensis Haas, 1973, Jungpleistozän, Qafze, Layer 17, Israel, [KOE 1539, det. E. Tchernov]
"Peridyromys" brailloni (Thaler, 1966), Petersbuch 2, Fränkische Alb, Mittelmiozän (MN4), [KOE 1549, 1562 ex BSPM]

Seleviniidae

Selevinia betpakdalaensis Belosludov und Bashanov, 1938; rezent, Kazakhstan, Karagandinskaia obl. Ulutau, [KOE 912 ex ZMM S-110990 leg. I. Stogov 1977]
Selevinia betpakdalaensis Belosludov und Bashanov, 1938; rezent, Kazakhstan, Dzherkazganskaia obl. 40 km S of Karsakpái, [KOE 913 ex ZMM S-145124, leg. I Stogov 09.1977]
Plioselevinia gromovi Sulimski, 1962, Pliozän, Weze/Polen, [KOE 994 ex ZPP M.Z. VIII. Vm – 328/1]

Außer diesen hier speziell behandelten Gattungen wurden zum Vergleich Vertreter der Cricetidae, Dipodidae, Zapodidae, Spalacidae und Rhizomyidae untersucht, weil stellenweise auch dort eine Verstellung der HSB zu beobachten ist.

Der Schmelz der Schneidezähne von Nagetieren ist ein traditionelles Forschungsgebiet, aber mit dem Raster-Elektronen-Mikroskop (REM) können viele der Merkmale, die bereits von Tomes (1850), Korvenkontio (1934) und Wahlert (1968) aufgrund lichtoptischer Untersuchungen diskutiert wurden, besser abgesichert, vor allem aber durch zusätzliche Merkmale ergänzt werden.

Nach Koenigswald und Clemens (1992) kann die Analyse des Zahnschmelzes auf fünf Komplexiktätsebenen erfolgen: 1. Kristallite, 2. Schmelzprismen, 3. Schmelztypen, 4. Schmelzmuster und 5. Dentition. Für die Untersuchung zur Systematik der Gliroidea sind nur die drei höheren Ebenen wichtig: Schmelztypen, Schmelzmuster und Dentition. Die Schmelztypen werden durch die Ausrichtung der Schmelzprismen charakterisiert. Das Schmelzmuster beschreibt die räumliche Anordnung der verschiedenen Schmelztypen in einem Zahn. Die unterschiedlichen Schmelzmuster der verschiedenen Zahnpositionen werden auf der Ebene der Dentition beschrieben. Bei fast allen Nagetieren unterscheidet sich das Schmelzmuser in den Schneidezähnen von dem der Backenzähne (Koenigswald 1988), weil sie unterschiedliche Funktionseinheiten bilden. Bei den meisten Gliroidea finden sich sogar Unterschiede in den Schmelzmustern zwischen oberen und unteren Schneidezähnen.

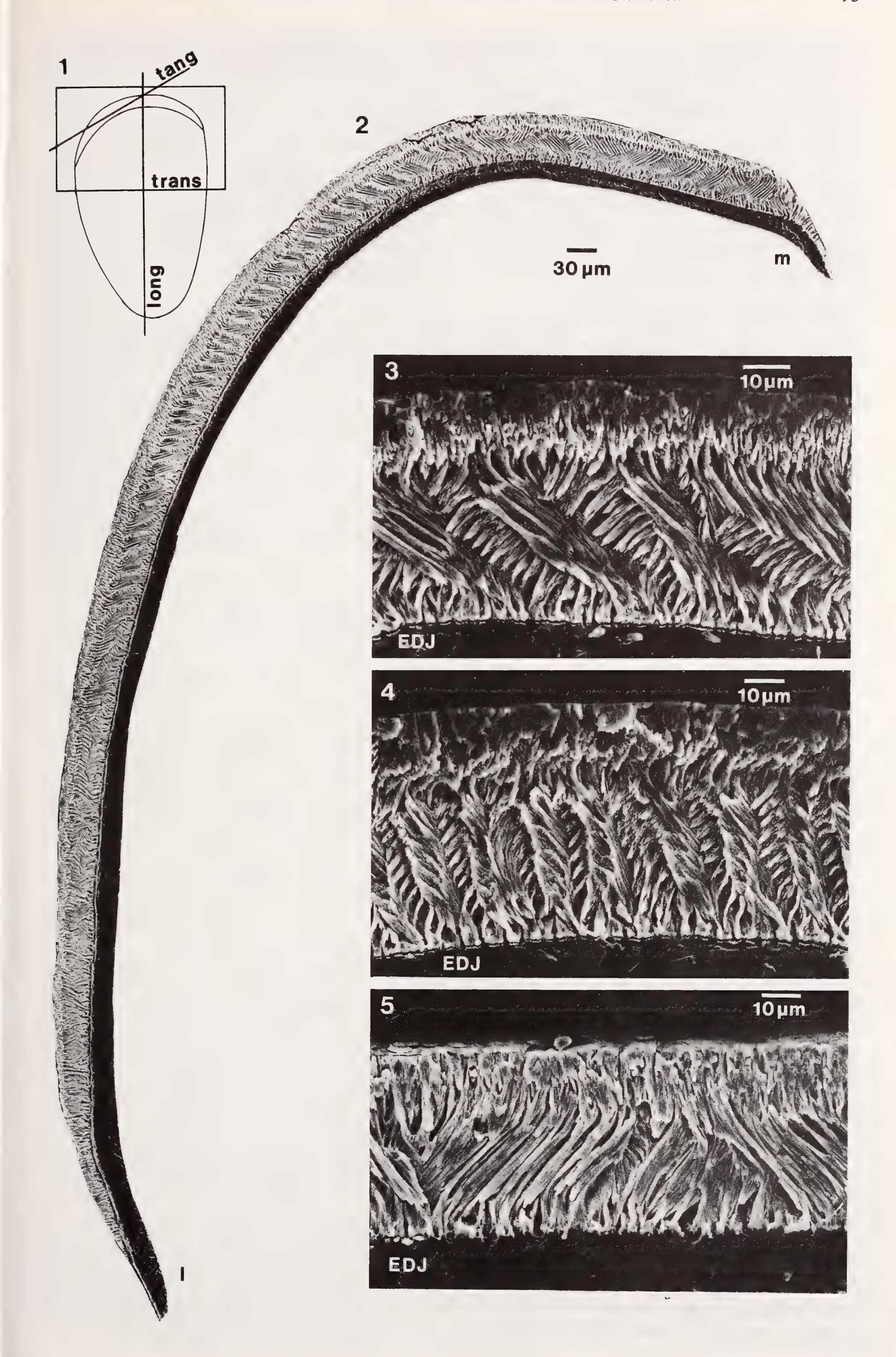
Die Analyse des Zahnschmelz erfordert je nach Fragestellung etwas unterschiedliche Präparationsmethoden. Für die hier interessierenden Schmelztypen und Schmelzmuster hat es sich als sinnvoll erwiesen, geätzte Anschliffe vom Zahnschmelz, nach Möglichkeit in den drei Hauptebenen (transversal, longitudinal und tangential; Wahlert und Koenigswald 1985) auszuwerten (Abb. 1).

Die trockenen Zähne fossiler oder rezenter Nagetiere werden zur leichteren Handhabung in Kunstharz eingebettet. Die gewünschte Schliffebene wird mit Schleifpulver der Körnung 1000 feingeschliffen und anschließend für 2–5 sec mit 2n HCl eingeätzt und unter fließendem Wasser sowie im Ultraschallbad gereinigt. Die kurze Ätzung mit einer relativ starken Säure legt die Prismen frei und erlaubt deren Richtung zu analysieren, selbst wenn die Prismen etwas angegriffen werden.

Die auf diese Weise vorbereiteten Präparate können nun zuerst unter dem Auflicht-Mikroskop, möglichst im Dunkelfeld, untersucht werden. Bei etwa 400facher Vergrößerung gewinnt man einen guten Überblick über die Ausrichtung der Schmelzprismen und damit die Verteilung der Schmelztypen. Für die weitere Untersuchung unter dem REM ist eine Bedampfung erforderlich. Auch nach der Bedampfung lohnt sich wiederum die Untersuchung im Auflicht-Mikroskop mit Dunkelfeldeinrichtung. Im REM kann bei niedriger Vergrößerung die Richtung der Prismen und bei höherer Vergrößerung (etwa 1000×) auch die Ausrichtung der interprismatischen Matrix (IPM) beobachtet

---

Abb. 1–5. 1. Orientierung der bevorzugten Schnittebenen zur Untersuchung des Schmelzes an Nagetierschneidezähnen (transversal, longitudinal und tangential). 2–5 *Myoxus glis,* transversale Schnitte durch den unteren Schneidezahn im SEM; 2 Das Übersichtsmosaik zeigt die wechselnde Schnittlage der Hunter-Schreger-Bänder (HSB) in der Portio interna (PI) (m = mesial; l = lateral); 3 Ausschnitt aus dem mesialen Bereich mit streng transversal orientierten HSB; 4 Ausschnitt aus dem mittleren Bereich mit leicht schräggestellten HSB; 5 Ausschnitt aus dem lateralen Bereich mit transversal orientierten HSB. Man beachte die dicke PLEX (EDJ = Schmelz-Dentin-Grenze)


1
tang
trans
long
2
30 µm
m
l
3
10 µm
EDJ
4
10 µm
EDJ
5
10 µm
EDJ

werden. Das REM bietet die Möglichkeit einer guten Fotodokumentation. Da bei stärkeren Vergrößerungen das Blickfeld immer kleiner wird, ist es schwieriger, die Gesamtstruktur im Auge zu behalten.

Für die Gliroidea ist die Ausrichtung der uniserialen Hunter-Schreger-Bänder (HSB) der Portio interna (PI) in den unteren Schneidezähnen von besonderer Bedeutung. Die Ausrichtung läßt sich bereits am Zahnquerschnitt durch den unterschiedlich breiten Ausbiß der Bänder abschätzen, sollte aber im tangentialen Anschliff geprüft werden. Da die Schräglage der HSB bei einigen Gattungen von lateral nach mesial wechseln kann, sind Mosaike, die den ganzen Zahnquerschnitt bei etwa 300facher Vergrößerung zeigen, erforderlich. Sie sind aber nicht mehr publizierbar, da die Verkleinerung auf Tafelformat wesentliche Einzelheiten verschwinden läßt (Abb. 2). Als Arbeitsgrundlage sind diese Mosaike aber sehr hilfreich, sowohl um die Unterschiede im Schmelzband von lateral nach mesial sicher erfassen und repräsentative Stellen für die Abbildungen auswählen zu können.

Jedes biologische Merkmal zeigt eine gewisse Variablität. Deswegen sollte am Material einer häufigen Gattung die Variabilität des untersuchten Merkmalskomplexes geprüft werden. Bisherige Untersuchungen haben gezeigt, daß auf der Ebene der Schmelzmuster die Variabilität so gering ist, daß in der Regel bereis die Analyse eines einzelnen Zahnes reproduzierbare Ergebnisse erbringt. Das erlaubt auch seltenes Material, sei es fossil oder rezent, in die Untersuchungen einzubeziehen. Die angewendete Methodik setzt eine gewisse Materialzerstörung voraus. Methoden einer zerstörungsfreien Schmelzanalyse, wie sie Boyde und Martin (1984) mit dem Tandem Scanning Reflected Light Microscope beschrieben haben, erfaßt aus der komplexen Struktur des Schmelzes lediglich die Prismenquerschnitte nahe der Außenkante des Schmelzes, die für die hier diskutierte Fragestellung von ganz untergeordneter Bedeutung sind.

Verwendete Abkürzungen und Spezialbegriffe

EDJ = Schmelz-Dentin-Grenze (= Enamel-dentine junction)
HSB = Hunter-Schreger-Bänder, Lagen von Prismen, die sich in einem großen Winkel überkreuzen
multiseriale HSB = HSB, deren Lagen mehrere Prismenquerschnitte dick sind
uniseriale HSB = HSB, deren Lagen nur einen Prismenquerschnitt dick sind
Inklination = Neigung der HSB gegen die EDJ im longitudinalen Schnitt, gemessen von der Normalen (Korvenkontio 1934)
IPM = Interprismatische Matrix, Kristallite, die keinen Prismen zuzuordnen sind (Wahlert und Koenigswald 1985)
MN = Säugetierzonen des Neogens
PE = Portio externa (Korvenkontio 1934), äußere Schmelzschicht in den Inzisiven der Nagetiere
PI = Portio interna (Korvenkontio 1934), innere Schmelzschicht der Nagetieren-Inzisiven
PLEX = Prismenloser Außenschmelz (Martin 1992)
Prismen = Bündel von Schmelzkristalliten, die den Schmelz höherer Säugetiere kennzeichnen
REM = Raster-Elektronen-Mikroskop
Schmelzmuster = räumliche Anordnung ein oder mehrerer Schmelztypen im Zahn (Koenigswald 1977)
Schmelztyp = Schmelzbereich, der durch eine einheitliche Prismenrichtung gekennzeichnet ist (Koenigswald 1977)

Herkunft der Materialien

NHMB = Naturhistorisches Museum Basel
BSPM = Bayerische Staatssammlung für Hist. Geol. u. Paläontologie, München
KOE = Schmelzsammlung Koenigswald, Univ. Bonn
SMF = Senckenberg-Museum, Frankfurt a. M.
SMNS = Staatl. Museum für Naturkunde, Stuttgart
ZPP = Paläozool. Institut der Polnischen Akademie, Warschau
ZMM = Zoologisches Museum, Moskau

Ergebnisse

Trotz der großen Zeitspanne, die das vorliegende Material abdeckt, lassen sich die untersuchten Arten nach dem Schmelzmuster der unteren Inzisiven zwanglos in drei Gruppen aufteilen. Um Wiederholungen zu vermeiden, wird jeweils zuerst das Grundmuster jeder Gruppe beschrieben und dann unter den einzelnen Arten nur die jeweiligen Abweichungen, Dickenverhältnisse von PI und PE sowie Besonderheiten angeführt.

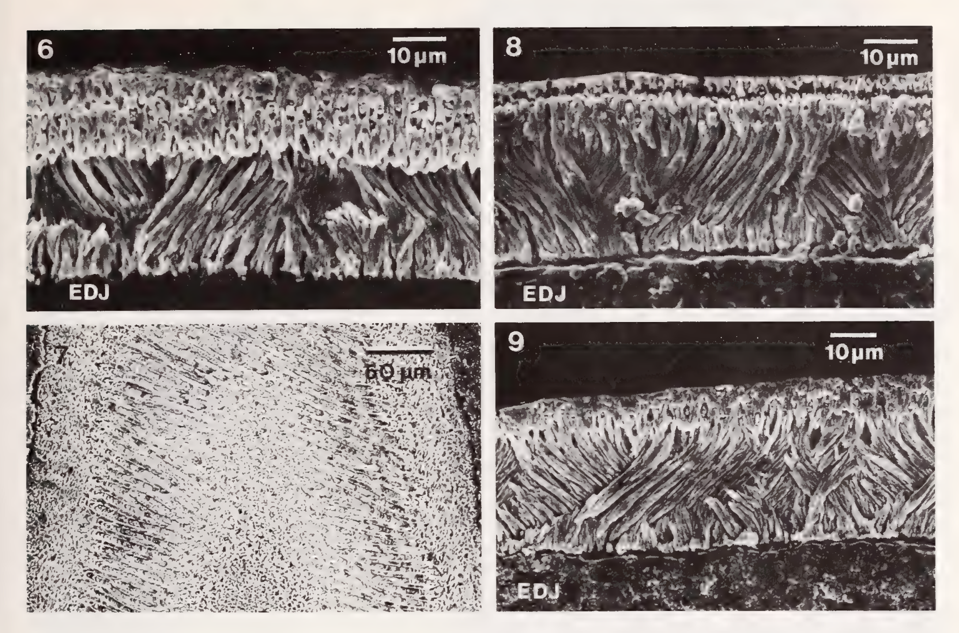


Abb.6–9. Schmelzmuster in den Schneidezähnen der Gruppe 1 der Gliroidea. 6 *Myoxus glis,* Schmelzmuster des oberen Inzisivs mit transversal angeordneten HSB im transversalen Schnitt; 7 *Myoxus glis,* leicht schräg gestellte HSB der PI im mittleren Bereich des Schmelzbandes im tangentialen Anschliff. Die Zahnachse steht senkrecht, die Zahnspitze liegt oben. Die PE ist am linken und rechten Rand sichtbar; 8 *Glirulus japonicus,* Schmelzmuster des oberen Inzisivs mit transversalen HSB; 9 *Glirulus japonicus,* Schmelzmuster durch den unteren Inzisiv mit transversalen HSB und einer dicken PLEX. (EDJ = Schmelz-Dentin-Grenze)

Das Schmelzmuster der meisten Nagetier-Schneidezähne umfaßt zwei Schichten, die seit Korvenkontio (1934) als Portio interna (PI) und Portio externa (PE) bezeichnet werden, die von unterschiedlichen Schmelztypen gebildet werden.

Gruppe 1 mit transversalen HSB und dicker PLEX

Das Schmelzmuster des unteren Schneidezahnes ist zweischichtig. Die PI wird von grundsätzlich transversal ausgerichteten, uniserialen HSB gebildet. Etwa auf der Mitte zwischen dem lateralen und dem mesialen Rand kommt es zu einer leichten Schrägstellung der HSB, die aber im tangentialen Schliff kaum auffällt. Die IPM liegt parallel zu den Prismen. An der scharfen Grenze zur PE biegen die Prismen in radiale Richtung und gleichzeitig tritt die IPM in einen Winkel zu den Prismen. Die Prismen nehmen schnell an Dicke ab und gehen in der IPM auf, so daß sich eine dicke prismenlose Außenschicht (PLEX) bildet (Abb. 2–5, 7–9).

Die oberen Schneidezähne zeigen ein sehr ähnliches Schmelzmuster allerdings mit streng transversal angeordneten HSB ohne jede Schrägstellung (Abb. 6).

Dieses Schmelzmuster wurde bei folgenden Taxa angetroffen:

Glirulus japonicus

Das Schmelzmuster des unteren Schneidezahnes wird von weitgehend transversal ausgerichteten HSB gekennzeichnet. Nur im mittleren Bereich zwischen dem lateralen und medialen Rand kommt es zu einer ganz leichten Schrägstellung. Die HSB stehen nach der

Überprüfung im Längsschnitt senkrecht auf der Schmelz-Dentin-Grenze (EDJ). Die PE nimmt etwa ¼ der Schmelzdicke ein (Abb. 8).

Der Querschnitt der oberen Inzisiven unterscheidet sich von dem der unteren durch eine abgeflachte labiale Seite und die schärferen Kanten an der mesialen wie lateralen Kante. Im Schmelzmuster besteht lediglich der Unterschied, daß die HSB über die ganze Länge streng transversal angeordnet sind (Abb. 9).

Myoxus glis

Das Schmelzmuster der unteren Inzisiven ist durch weitgehend transversale HSB gekennzeichnet (Abb. 2–5). Nur im mittleren Bereich, der etwas ausgeprägter ist als bei dem vorliegenden Zahn von *Glirulus,* ist eine leichte Schrägstellung der HSB sichtbar. Nach einem tangentialen Schliff läßt die Schrägstellung von rund 20° die HSB apikal zur mesialen Seite hin ansteigen (Abb. 7). Nach mehreren Längsschnitten zu schließen, stehen die HSB nahezu senkrecht auf der Schmelzdentingrenze (EDJ). Die PE nimmt ¼ der Schmelzdicke ein. Die Prismen biegen sich in die radiale Richtung um, verschwinden aber sehr schnell in einer dicken PLEX (Abb. 3–5).

Das Schmelzmuster von oberen Inzisiven zeigt streng transversale HSB (Abb. 6). Die PE, die ewa ⅓ der Schmelzdicke einnimmt, wird im innersten Bereich von radialem Schmelz gebildet, die Prismen verschwinden aber sehr schnell in einer dicken PLEX.

Nachtrag während des Drucks:

Gliravus sp.

Das Schmelzmuster des unteren Inzisiven zeigt weitgehend transversale HSB, die im mittleren Bereich eine leichte Schrägstellung erfahren. Die IPM liegt parallel zu den Prismen. Die Portio Externa ist sehr dünn und wird weitgehend von prismenlosem Schmelz (PLEX) gebildet. – *Gliravus* sp. [Koe 1639] aus dem Oligozän von Le Bretou (MN 32), ist der älteste Vertreter der hier untersuchten Gliriden und gehört eindeutig zur Gruppe 1. Da mir dieser Zahn erst nach der Fahnenkorrektur zugänglich wurde, konnte *Gliravus* weder in Material-Liste und Text noch in Abb. 29 angeführt werden.

Gruppe 2 mit diagonalen HSB

Das Schmelzmuster der unteren Schneidezähne wird von durchgehend diagonal ausgerichteten HSB in der PI gekennzeichnet. Die uniserialen HSB steigen in ihrer seitlichen Erstreckung von lateral nach mesiad mit einem Winkel von maximal 45° an (Abb. 10–11). Die stärkste Schrägstellung liegt etwa in der Mitte zwischen dem lateralen und dem mesialen Rand des Schmelzbandes. Sowohl im lateralen wie im mesialen Randbereich flacht die Stellung der HSB ab, ist aber immer noch geneigt. Die IPM liegt in der PI parallel zu den Prismen. Die PE wird von radialem Schmelz gebildet. Auffallenderweise stehen die Prismen aber nicht in Richtung der Zahnachse, sondern stehen senkrecht zu den geneigten HSB, das heißt, sie sind nach laterad gekippt. Die IPM steht im Winkel zu den Prismen und anastomosiert zwischen ihnen. Eine PLEX ist sehr dünn, wenn üerhaupt vorhanden (Abb. 12–13, 14–17).

Das Schmelzmuster der oberen Schneidezähne zeigt in der PI uniseriale HSB, die transversal ausgerichtet sind. Die PE wird von radialem Schmelz gebildet. Eine Reduktion der Prismen in der Außenschicht ist nicht zu beobachten. Die PLEX ist sehr dünn oder gar nicht ausgebildet (Abb. 14).

Dieses Schmelzmuster wurde bei den folgenden Arten gefunden:

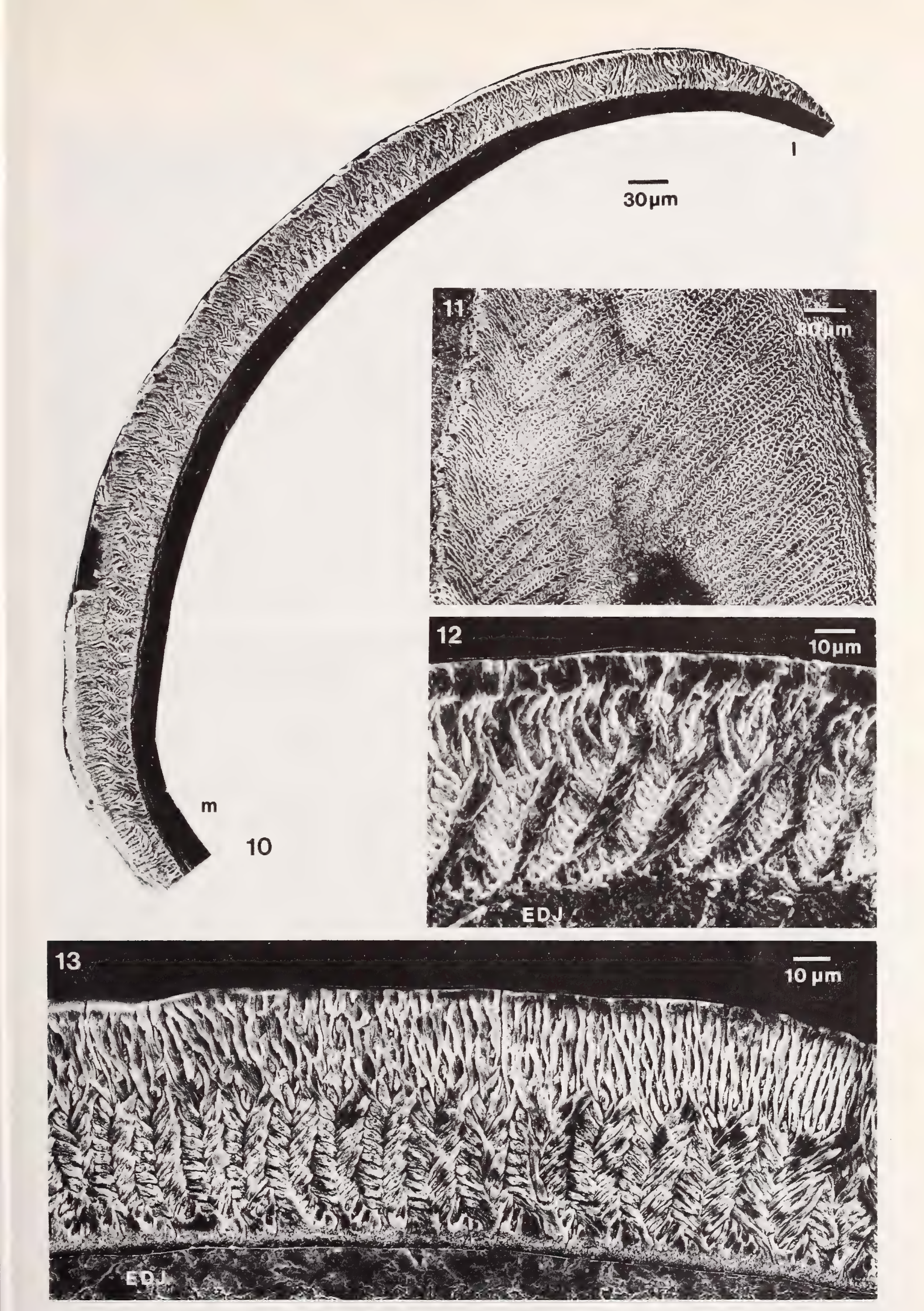


Abb. 10–13. Schmelzmuster in den unteren Schneidezähnen der Gruppe 2 der Gliroidea. 10 Transversaler Schnitt durch den unteren Inzisiv von *Dryomys nitedula* mit durchgehend diagonal gestellten HSB in der PI (m = mesial; l = lateral); 11 im tangentialen Schnitt durch den unteren Inzisiv von *Dryomys nitedula* zeigt sich die Schrägstellung der HSB von etwa 45°; 12 transversaler Schnitt durch den unteren Inzisiv von *Dryomys nitedula;* 13 transversaler Schnitt durch den unteren Inzisiv von *Eliomys (Tyrrhenoglis) majori.* (EDJ = Schmelz-Dentin-Grenze)

Anthracoglis marinoi

Die schräg gestellten HSB der PI verflachen nur am mesialen Rand etwas. Die PE mit radialem Schmelz nimmt etwas mehr als ⅓ der Schmelzdicke ein. Eine PLEX ist nur ganz dünn ausgebildet.

Dryomys nitedula

Im Schmelzmuster des unteren Schneidezahnes sind die HSB der PI durchgehend diagonal angeordnet (Abb. 10). Die Bänder steigen in der Mitte mit etwa 45° an (Abb. 11). Im lateralen Randbereich des Schmelzes verflacht die Schrägstellung etwas. Bei *Dryomys* hat der obere Schneidezahn auf der lateralen Seite eine Einkerbung, die aber nur in der vorderen Hälfte noch vom Schmelz überdeckt ist. Im Schmelz des oberen Schneidezahnes ist die PE mit radialem Schmelz dick und zeigt eine dünne, aber deutlich abgesetzte PLEX.

Eliomys quercinus

Das Schmelzmuster kennzeichnen die durchgehend diagonal zur Längsachse angeordneten HSB der PI. In der PE, die etwas mehr als ⅓ der Schmelzdicke einnimmt, zeigt die geringe Ätzung, daß die Prismen im radialen Schmelz der PE an Dicke abnehmen und in der immer dicker werdenden IPM, die die PLEX bildet, verschwinden. Die PLEX selber nimmt etwa ¾ der PE ein (Abb. 16).

Im Schmelzmuster des oberen Inzisivs nimmt die PE etwa ⅓ bis ¼ der Schmelzdicke ein. Die PLEX ist sehr dünn.

Eliomys (Hypnomys) sp.

Im Schmelzmuster der unteren Inzisiven sind die HSB der PI gleichmäßig und zwar von lateral bis mesial durchgehend, aber nur wenig schräggestellt. Gemessen wurden im tangentialen Schliff 20°. Auf die PE entfällt etwa ¼ der Schmelzdicke. Die PLEX ist dünn und entspricht der rot gefärbten Außenschicht.

Die oberen Inzisiven weisen streng transversal ausgerichtete HSB auf. Die PE nimmt nur ewa ¼ der Schmelzdicke ein. Die PLEX ist nur dünn ausgebildet.

Eliomys (Maltamys) wiedincitensis

Der untere Inzisiv zeigt die durchgehend diagonal ausgerichtete HSB. Im tangentialen Schliff wurden für den Anstieg etwa 45° gemessen. Die PE nimmt etwa ⅓ der Schmelzdicke ein. Eine PLEX ist nur ganz dünn vorhanden (Abb. 17). Es lag kein oberer Inzisiv vor.

Eliomys (Maltamys) gollcheri

Im unteren Schneidezahn verflachen die schräggestellten HSB zur mesialen Seite hin, so daß sie hier fast transversal liegen. Die PE erreicht auf der labialen Seite ⅓ der Schmelzdicke, ist in den anderen Bereichen etwas dünner. Eine PLEX ist kaum ausgebildet.

Im Schmelzmuster der oberen Inzisiven sind die grundsätzlich transversalen HSB in der Mitte schwach aufgewölbt, so daß sie nach beiden Seiten hin leicht schräggestellt sind. Die PE nimmt gut ⅓ der Schmelzdicke ein.

Eliomys (Tyrrhenoglis) majori

Im unteren Inzisiv sind die HSB der PI durchgehend schräg gestellt (Abb. 13). Im medialen Teil nimmt die PE mit dem leicht gewinkelten radialen Schmelz etwas mehr als ⅓ der Schmelzdicke ein. Eine PLEX ist nur ganz dünn ausgebildet.

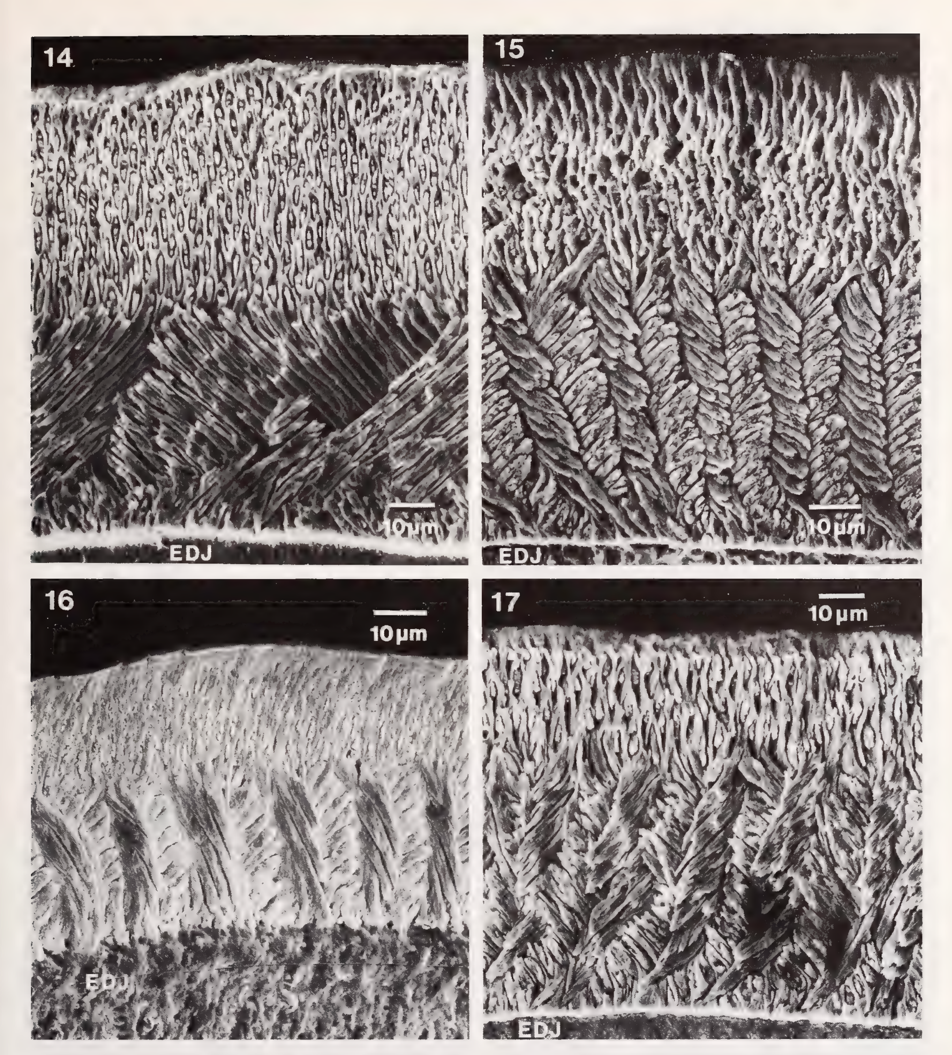


Abb. 14–17. Schmelzmuster in den Schneidezähnen der Gruppe 2 der Gliroidea in Transversalschnitten. 14 *Leithia* sp., Schmelzmuster des oberen Inzisivs mit transversalen HSB in der PI, die Interprismatische Matrix (IPM) begleitet die Prismen. Die PE wird von radialem Schmelz gebildet; 15 *Leithia* sp., Schmelzmuster des unteren Inzisivs mit diagonal gestellten HSB in der PI; 16 *Eliomys quercinus,* Schmelzmuster des unteren Inzisivs; 17 *Eliomys (Maltamys) wiedincitensis,* Schmelzmuster des unteren Inzisivs. (EDJ = Schmelz-Dentin-Grenze)

Leithia melitensis

Die Schrägstellung der HSB zeigt der transversale Anschliff (Abb. 15). Das Gesamtmosaik läßt eine Verflachung zum lateralen Rand erkennen. In einem tangentialen Schliff konnte die maximale Schrägstellung mit etwa 45° gemessen werden. Im oberen Inzisiv liegen die HSB streng transversal und die PE erreicht fast ½ der Schmelzdicke (Abb. 14). Eine PLEX fehlt im unteren wie oberen Inzisiv.

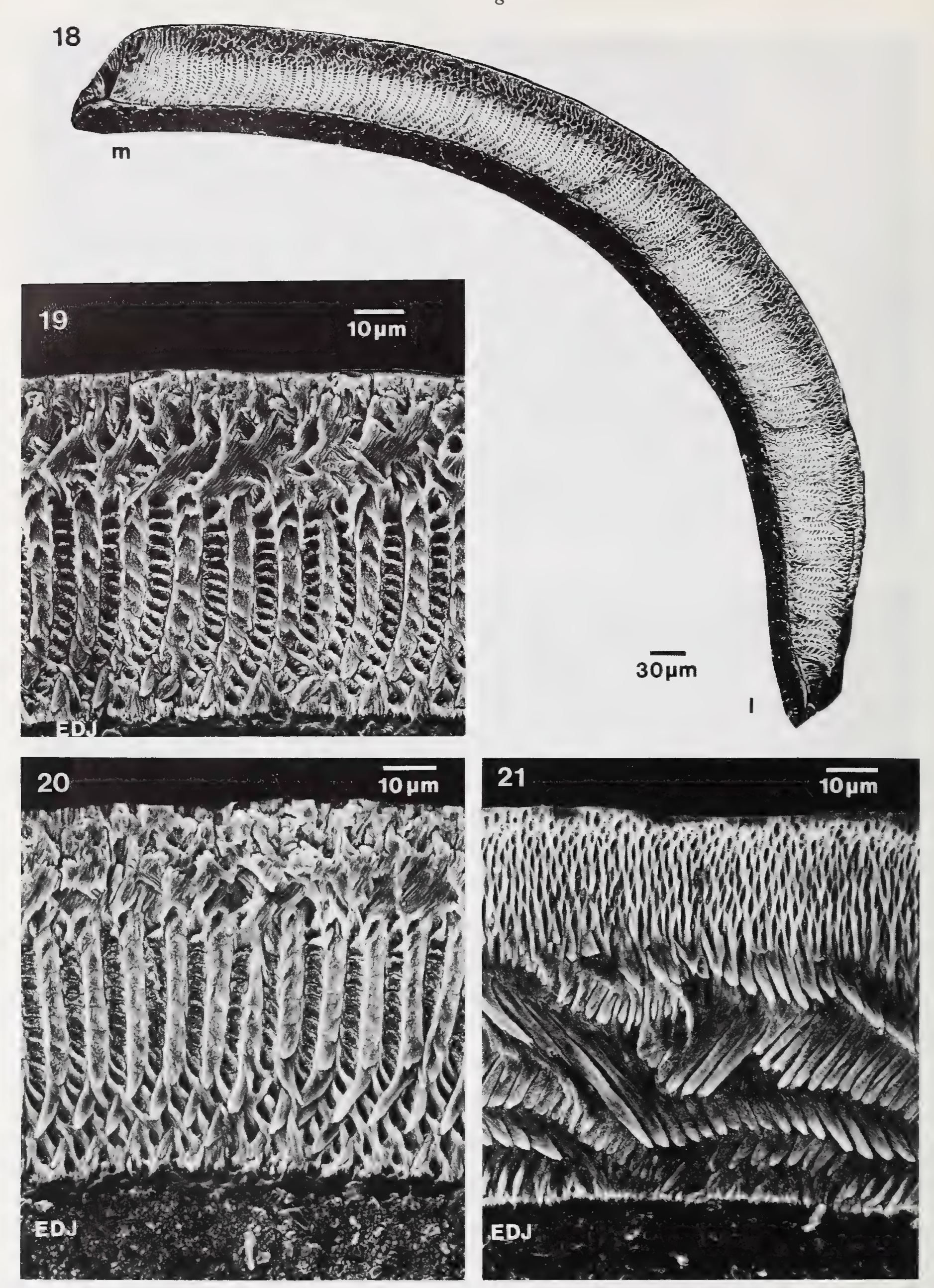


Abb. 18–21. Schmelzmuster in den Schneidezähnen der Gruppe 3 der Gliroidea in Transversalschnitten. 18 und 19 *Muscardinus avellanarius,* der Querschnitt durch den unteren Schneidezahn zeigt ein gleichförmiges Schmelzmuster von der mesialen zur lateralen Seite mit longitudinal ausgerichteten HSB in der PI ohne Umbiegungszone; 20 *Myomimus roachi,* Schmelzmuster des unteren Inzisivs mit longitudinalen HSB in der PI und tangentialem Schmelz in der PE; 21 *Myomimus roachi,* Schmelzmuster des oberen Inzisivs mit transversalen HSB in der PI und radialem Schmelz in der PE. (EDJ = Schmelz-Dentin-Grenze)

Microdyromys miocaenicus

Das Schmelzmuster des unteren Inzisiv von *Microdyromys* ist durch eine auffallend dicke PI mit durchgehend schräg gestellten HSB gekennzeichnet. Die PE ist so dünn, daß sich eine PE nicht ausgliedern läßt.

"Peridyromys" brailloni

Daams (1990) betont, daß *"P." brailloni* nicht von *Peridyromys murinus* herzuleiten ist. Deswegen bezieht sich die hier getroffene Zuordnung lediglich auf die Art *brailloni* nicht aber auf die Gattung *Peridyromys* allgemein.

Die HSB sind durchgehend diagonal gestellt, wenn sie auch in den Randbereichen erheblich verflachen. Die PE nimmt etwa ⅓ der Schmelzdicke ein. Im Gegensatz zu *Myoxus* und *Glirulus* ist die PLEX ganz dünn.

Gruppe 3 mit longitudinalen HSB

Das Schmelzmuster der unteren Inzisiven ist in der dritten Gruppe durch longitudinal ausgerichtete HSB in der PI gekennzeichnet (Abb. 18). Während die Prismen des einen Bandes apikal aufsteigen, sinken die der benachbarten Bänder in der Gegenrichtung ab (Abb. 19). Die IPM liegt grundsätzlich parallel zu den Prismen, kann aber bei einigen Formen eine Innenzone markieren, in der die IPM deutlich im Winkel zu den Prismen steht. Die PE wird von tangentialem Schmelz gebildet (Abb. 19–20, 23–24, 26). Das heißt, die Prismen bleiben in der transversalen Ebene und weisen nach mesiad. Die IPM bleibt ebenfalls in der transversalen Ebene, steht aber im rechten Winkel zu den Prismen und anastomosiert zwischen diesen. Die PLEX bleibt meist nur dünn ausgebildet.

Das Schmelzmuster der oberen Inzisiven wird von grundsätzlich transversal ausgerichteten HSB gebildet (Abb. 21–22), in der die IPM parallel zu den Prismen liegt. Die PE wird wie üblich von radialem Schmelz gebildet, der von einer dünnen PLEX überlagert sein kann.

Dieses Schmelzmuster wurde bei den folgenden Arten gefunden:

Graphiurus murinus

Im Querschnitt des unteren Schneidezahnes treten die longitudinal angeordneten HSB der PI hervor. Die IPM steht nur in einer ganz dünnen Innenzone im Winkel zu den Prismen. Der PE fällt in der Zahnmitte fast ½ der Schmelzdicke zu. Eine PLEX ist nur ganz dünn ausgebildet (Abb. 26).

Im oberen Inzisiv sind die HSB der PI transversal ausgerichtete, aber am lateralen wie mesialen Rand leicht schräg gestellt. Die PE ist dünn und weist eine deutliche Außenzone mit prismenlosem Schmelz auf (PLEX).

Miodyromys aegercii und biradiculus

Im Schmelzmuster der unteren Schneidezähne bildet innerhalb der longitudinal ausgerichteten HSB die gewinkelt zu den Prismen stehende IPM eine Innenzone, die etwa ⅓ bis ½ der Dicke der PI einnimmt und mit unscharfer Abgrenzung in die äußere Zone der PI übergeht. Auf die PE entfällt rund ⅓ der Schmelzdicke (Abb. 25).

Die oberen Schneidezähne zeigen transversale HSB in der PI und eine relativ dicke PE mit radialem Schmelz.

Muscardinus avellanarius

Die uniserialen HSB der PI sind parallel zur Längsachse, also longitudinal angeordnet (Abb. 18–19). Die IPM markiert undeutlich zwei nahezu gleich starke Zonen. In der etwas

schwächeren Innenschicht steht die IPM deutlich im Winkel zu den Prismen, während sie in den übrigen Bereichen der HSB die Prismen begleitet. Im Querschnitt neigen sich die HSB in der Innenschicht leicht nach lateral, schwenken aber dort, wo die IPM verschwindet, in die Richtung senkrecht zur EDJ um. Der Übergang zur PE mit ihrem tangentialen Schmelz ist scharf. Die Prismen verschwinden erst dicht an der Außenkante des Schmelzes, so daß die PLEX nur sehr dünn ist.

Die longitudinale Anordnung der HSB sowie der tangentiale Schmelz der PE im unteren Inzisiv wurde durch Längsschnitte eindeutig bestätigt.

Im oberen Inzisiv sind die HSB der PI transversal orientiert, besitzen aber eine deutlich stärkere Inklination gegenüber der EDJ als bei den meisten anderen Gliriden. Die dicke PE nimmt etwa ⅓ der Schmelzdicke ein. Eine PLEX ist nur ganz dünn ausgebildet.

Myomimus roachi und Myomimus gafzensis

Die longitudinale Ausrichtung der HSB wurde im Längsschliff bestätigt. Die IPM markiert eine deutliche Innenzone innerhalb der PI (Abb. 20). Die PLEX ist unbedeutend. In den oberen Inzisiven nimmt die PE etwa ¼ der Schmelzdicke ein. Eine PLEX ist kaum vorhanden (Abb. 21).

Plioselevinia gromovi

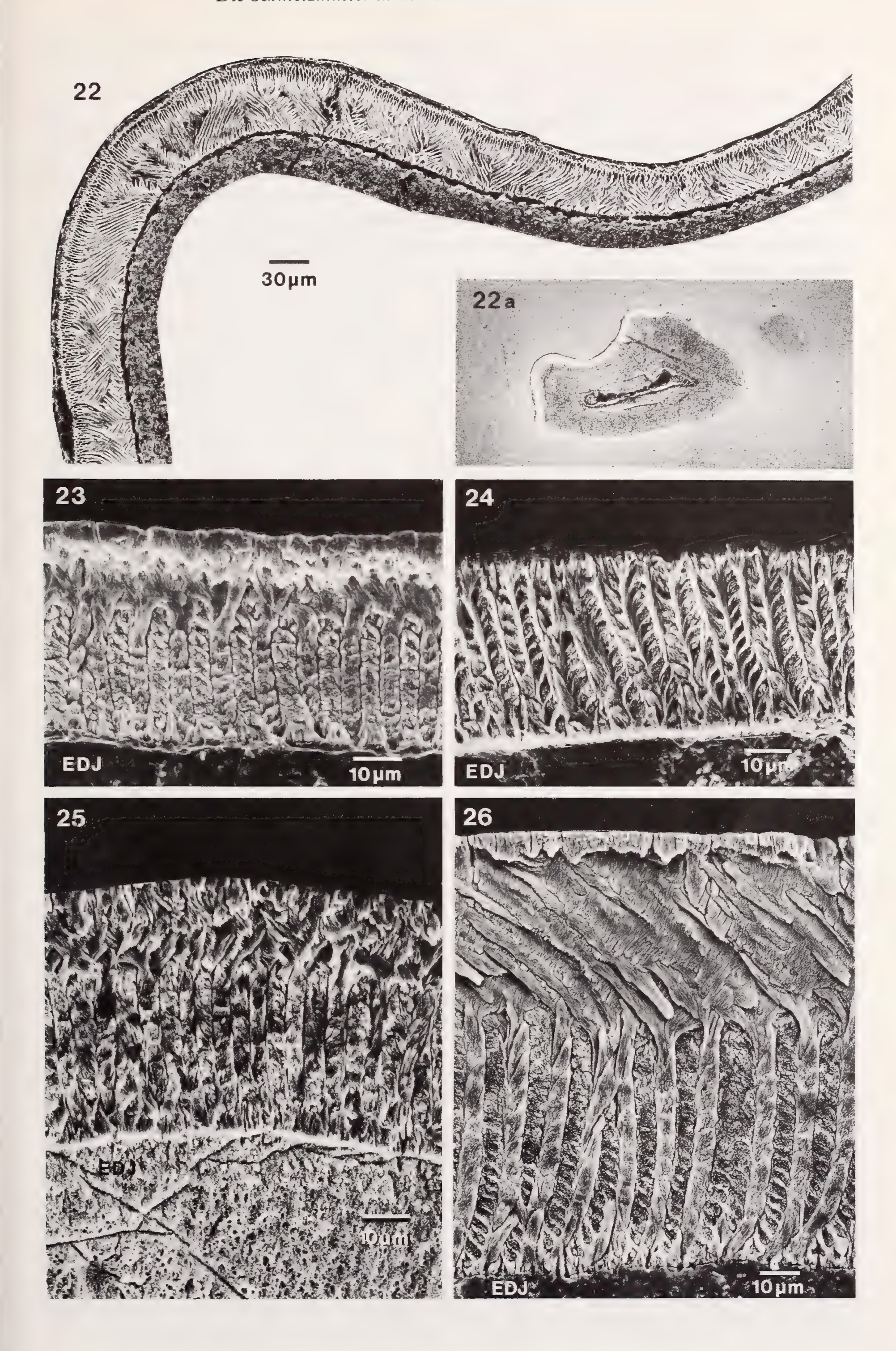
Von *Plioselevinia* konnte eine dünne Scheibe des unteren Schneidezahnes untersucht werden. Diese zeigt die longitudinal angeordneten HSB (Abb. 24), die an den Seiten leicht schräg gestellt sind. Die IPM formt eine Innenzone, die etwa ⅓ bis ½ der Dicke der PI einnimmt. Die PE ist in der vorhandenen Zahnscheibe reduziert, und die Prismen gehen von den HSB unmittelbar in eine dünne PLEX über.

Selevinia betpakdalaensis

Im Schmelzmuster des unteren Schneidezahnes stehen die HSB der PI longitudinal, wie es bei *Muscardinus* oder *Myomimus* zu beobachten ist (Abb. 23). Die IPM verläuft weitgehend parallel zu den Prismen und läßt keine Innenzone durch eine auffallende Winkelstellung erkennen. Die PE wird eindeutig aus tangentialem Schmelz gebildet, damit fügt sich *Selevinia* völlig in das typische Bild der Gruppe 3. Die PLEX nimmt etwa ⅓ der PE ein (Abb. 23).

Der obere Inzisiv besitzt eine tiefe Außenfurche (Abb. 22), die auf der labial/lateralen Seite liegt und ganz mit Schmelz überdeckt ist. Der obere Schneidezahn zeigt trotz seiner starken Außenfurche ein einheitliches Schmelzmuster. Die PI wird von transversal angeordneten HSB gebildet (Abb. 22). Auf die PE entfallen etwa ¼ der Schmelzdicke. Etwa in der halben Dicke der PE verschwinden die Prismen in der PLEX.

Abb. 22–26. Schmelzmuster in den Schneidezähnen der Gruppe 3 der Gliroidea in Transversalschnitten. 22 *Selevinia betpakdalaensis,* Zahnquerschnitt und Schmelzmuster des oberen Inzisivs, mit transversalen HSB und radialem Schmelz in der PE. Das Mosaik zeigt die Aufwölbung mesial der großen Längsfurche; 23 *Selevinia betpakdalaensis,* Schmelzmuster des unteren Inzisivs mit longitudinalen HSB in der PI und tangentialem Schmelz in der PE; 24 *Plioselevinia gromovi,* Schmelzmuster im unteren Inzisiv, sichtbar sind die Longitudinalen HSB, die PE scheint reduziert zu sein; 25 *Miodyromys aegercii,* Schmelzmuster des unteren Inzisivs mit longitudinalen HSB und tangentialem Schmelz in der PE; 26 *Graphiurus* sp., Schmelzmuster des unteren Inzisivs mit longitudinalen HSB in der PI und einem besonders dicken tangentialen Schmelz in der PE. (EDJ = Schmelz-Dentin-Grenze)


22
30µm
22a
23
EDJ
10µm
24
EDJ
10µm
25
EDJ
10µm
26
EDJ
10µm

Diskussion

Die Gliridae sind eine recht alte Gruppe, die bereits im Oligozän und frühen Miozän eine starke Radiation erfahren hat. Von dieser Vielfalt ist in der rezenten Fauna nur noch ein kleiner Ausschnitt überliefert. Die Gliridae treten erstmals mit *Eogliravus* im Mittel-Eozän auf. Von *Gliravus*, der im Ober-Eozän und Oligozän belegt ist, geht die große Radiation aus. Die rezenten Gattungen lassen sich z. T. bis in das untere Miozän zurückverfolgen: *Myomimus* ist seit dem Unter-Miozän im Mittelmeerraum belegt (Daams 1981). *Myoxus* (= *Glis*) wird erstmals im untersten Miozän (MN1) (Mayr 1979), *Glirulus* aus MN3 (Meulen und Bruijn 1982) genannt; *Eliomys* und *Muscardinus* sind in Süddeutschland im Mittel-Miozän ab MN9 belegt (Mayr 1979). Diese Gattungen werden allerdings von zahlreichen anderen und nur fossil bekannten Gliriden begleitet, von denen nur einige hier auf das Schmelzmuster hin untersucht werden konnten.

Das Schmelzmuster der Inzisiven zeigt innerhalb der Gliroidea eine größere Vielfalt als bei fast allen anderen Nagergruppen. Meist unterscheidet sich beim gleichen Individuum das Schmelzmuster des unteren Inzisivs von dem des oberen. Während die oberen Inzisiven aller Gattungen im Schmelzmuster sehr einheitlich sind, lassen sich an den unteren Inzisiven drei Gruppen unterscheiden, die durch transversal, diagonal bzw. longitudinal angeordnete HSB in der PI gekennzeichnet sind. Die Unterschiede im Schmelzmuster liegen etwa im Gattungsniveau oder höher, denn verschiedene Arten einer Gattung *Myomimus* zeigen das gleiche Schmelzmuster. Auch in den verschiedenen Untergattungen von *Eliomys* wurden keine wesentlichen Unterschiede gefunden. Die weitere Diskussion kann deswegen auf der Gattungsebene erfolgen. Um die Evolutionsrichtung zu ermitteln muß ein Vergleich mit den Schneidezähnen anderer Nagetiere geführt werden.

Ursprüngliche Schmelzmuster und Richtung der Merkmalsverschiebung

Das vorliegende Material erlaubt zwar keine Analyse der fossilen Vorläuferformen der Gliriden, die Hartenberger (1971) bei *Microparamys* vermutet. Um festzustellen, welche Merkmale im Schmelzmuster ursprünglich und welche als abgeleitet zu bewerten sind, müssen die wichtigsten Merkmale der Schmelzmuster bei den anderen Nagetieren als Außengruppe betrachtet werden.

Bei Caviomorpha und Hystricomorpha stellte Martin (1992) lediglich transversal angeordnete (multiseriale) HSB in der PI fest. Die PE wird grundsätzlich von radialem Schmelz gebildet. Unterschiede zwischen unteren und oberen Inzisiven wurden nicht gefunden.

Auch bei den Sciuromorpha ließen sich bislang keine Unterschiede zwischen unteren und oberen Inzisiven finden. Die (uniserialen) HSB sind ebenfalls grundsätzlich transversal angeordnet, lediglich für *Cynomys* beschreibt Korvenkontio (1934) ein leichtes Aufbiegen der HSB zur Mitte. Die IPM begleitet die Prismen (Boyde 1978; Koenigswald 1990). Die PE wird aus radialem Schmelz gebildet.

Die meisten Myomorpha, zu denen hier auch die Gliroidea gerechnet werden, besitzen ebenfalls in der PI uniseriale HSB, die in der ursprünglichen Ausprägung transversal angeordnet sind. Die IPM ist ursprünglich parallel zu den Prismen ausgerichtet. Zu diesem Schmelzmuster gehört eine PE aus radialem Schmelz. Wesentliche Modifikationen treten allerdings sowohl in der Richtung der IPM wie in der Ausrichtung der HSB auf. Die IPM tritt zumindest in den unteren Schneidezähnen bei den Muridae, den Arvicolidae und den meisten Cricetidae in einen großen Winkel zu den Prismen und versteift so die dritte Raumrichtung (Koenigswald 1988). Abweichungen in der ursprünglich transversalen Anordnung der HSB zeigen außer den hier untersuchten Gliroidea einige Cricetidae (Myospalacinae und Platacanthomyinae), Rhizomyidae, Zapodidae und Dipodidae. Dabei treten regelmäßig große Unterschiede zwischen oberen und unteren Schneidezähnen auf.

Vertreter dieser Familien sollen weiter unten mit den Gliroidea verglichen werden.

Aus dieser Merkmalsverteilung kann man schließen, daß auch bei den Gliroidea ein Schmelzmuster für die Schneidezähne mit folgenden Merkmalen am Anfang steht:

1. obere und untere Schneidezähne unterscheiden sich nicht;
2. die HSB der PI sind transversal angeordnet;
3. die IPM begleitet die Prismen;
4. die PE wird aus radialem Schmelz gebildet;
5. die prismenlose Außenschicht (PLEX) ist dünn.

Diese ursprüngliche Merkmalskombination wird bei den Gliroidea in den oberen Inzisiven weitgehend beibehalten, ist aber in den unteren Inzisiven bei allen untersuchten Gliroidea bereits verändert.

Das auffälligste Merkmal ist die zunehmende Kippung der HSB in der PI. Aus der ursprünglich transversalen Anordnung läßt sich die beginnende Schrägstellung in der Gruppe 1 (*Glirulus* und *Myoxus*) ableiten. Als Autapomorphie zeigen diese beiden Gattungen eine starke Ausbildung der PLEX .

In der Gruppe 2 wird die Tendenz, die HSB schräg zu stellen, verstärkt und zeigt sich in der durchgehend diagonalen Anordnung der HSB. Verbunden ist damit die Kippung der Prismenrichtung im radialen Schmelz. Der Winkel zwischen HSB und PE bleibt erhalten. Dieses Merkmal hat besondere Bedeutung für den Vergleich mit anderen Nagern mit verstellten HSB.

In der Gruppe 3 sind die HSB so stark gekippt, daß sie longitudinal ausgerichtet sind. Da die ursprüngliche Winkelbeziehung zur PE bestehen bleibt, wird die PE von tangentialem Schmelz gebildet. Erst in diesem Niveau markiert bei einigen Gattungen die IPM durch ihre Winkelstellung eine Innenzone in der PI.

Es ist auffallend, daß bei dem bisherigen Material noch keine Übergangsformen zwischen den Gruppen 2 und 3 aufgetreten sind. Auch wenn bisher nur einige Gattungen aus dem fossilen Bereich untersucht werden konnten, spricht das dafür, daß die Trennung dieser drei Gruppen zeitlich noch weiter zurückliegt als die Herkunft des hier untersuchten Fossilmaterials. Wahrscheinlich sind diese drei Gruppen bereits zu Beginn des Miozäns getrennt.

Bisher ist es noch nicht gelungen, die Dicke der PE sinnvoll zu interpretieren. Die Reduktion der PE bei *Plioselevinia* ist auf jeden Fall ein stark abgeleitetes Merkmal. Die PLEX an der Außenseite der EP tritt bei Nagetieren regelmäßig auf und enthält die rot gefärbte Außenschicht. Die Verdickung der PLEX bei *Myoxus* und *Glirulus* ist ebenfalls als abgeleiteter Merkmalszustand zu betrachten.

Es ist höchst bemerkenswert, daß sich die Seleviniidae problemlos in die dritte Gruppe einordnen, obwohl sie in der Molarenmorphologie stark abweichen. Bevor die drei Gruppen mit den bisherigen systematischen Gliederungen der Gliroidea verglichen werden, ist die grundsätzliche Frage zu stellen, wie weit diese speziellen Merkmale des Schmelzmusters konvergent entstanden sein können.

Diagonale und longitudinale HSB in den Inzisiven anderer Nager

Das oben dargestellte Modell postuliert für die Gliroidea eine zunehmende Schrägstellung der HSB, die in der dritten Gruppe in longitudinaler Ausrichtung gipfelt. Es ist zu prüfen, ob es sich dabei um ein synapomorphes Merkmal handelt, oder ob es mehrfach parallel entstanden sein kann. Diese Frage kann am ehesten aus dem Vergleich mit jenen Gattungen der Myomorpha beantwortet werden, die ebenfalls eine modifizierte Anordnung der HSB in der PI besitzen.

Innerhalb der Myomorpha kommt es mehrfach zu einer Verstellung der ursprünglich transversalen HSB, bei der sich unterschiedliche Typen abgrenzen lassen. Bei *Tachyoryctes* (Rhizomyidae), *Spalax* (Spalacidae), *Myospalax* und *Prosiphneus* (Myospalacinae, Criceti-

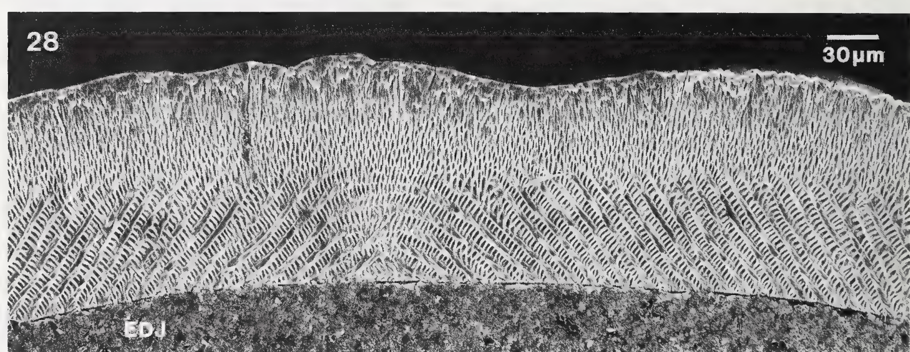


Abb. 27–28. 27 Alactagulus pumilo, (KOE 952, Syrien), Schmelzmuster des unteren Inzisivs mit longitudinalen HSB in „Fächerstellung" in der PI und tangentialem Schmelz in der PE. (m = mesial; l = lateral); 28 *Spalax ehrenbergi,* (KOE 916, Israel), Schmelzmuster des unteren Inzisivs im transversalen Schnitt mit longitudinalen HSB und einer deutlichen medialen Umbiegungszone in der PI. Die IPM steht in deutlichem Winkel zu den Prismen. Die PE wird von radialem Schmelz gebildet. (EDJ = Schmelz-Dentin-Grenze)

dae) steigen die HSB in der tangentialen Aufsicht von beiden Seiten apikal an und biegen in der Zahnmitte oder etwas seitlich davon um. Auch im transversalen Schnitt ist diese Umbiegung zu erkennen (Abb. 28). Die Verstellung der HSB kommt nur in den unteren Inzisiven vor. Mit diesem Typ der Verstellung der HSB haben die hier untersuchten

Gattungen der Gliroidea nichts zu tun, weil ihnen die mediale Umbiegungszone eindeutig fehlt.

Wahlert und Koenigswald (1985) haben longitudinale HSB für die unteren Schneidezähne der Eomyidae beschrieben, denen eine Umbiegungszone in der Mitte des Schmelzbandes fehlt. Eine weitere Übereinstimmung läßt sich mit der Gruppe 3 der Gliroidea feststellen, nämlich daß die PI bei den Eomyiden ähnlich wie bei *Muscardinus* oder *Miodyromys* zweigeteilt ist. In einer Innenzone steht die IPM im Winkel zu den Prismen, während sie in der äußeren Zone der PI die Prismen umhüllt. Allerdings ist die Winkelstellung zwischen beiden Zonen, die bei den Eomyiden beobachtet werden konnte (Wahlert und Koenigswald 1985), bei den Gliroidea nicht ausgebildet. Einen grundsätzlichen Unterschied gegenüber den Gliroidea zeigen die Eomyidae aber mit ihrem radialen Schmelz in der PE. Hier wird der ursprünglich radiale Schmelz beibehalten und nicht wie bei allen Gliroidea mitgedreht. Damit lassen sich die Übereinstimmungen im Schmelzmuster zwischen den Eomyiden und der dritten Gruppe der Gliroidea als Parallelentwicklung erkennen. Obere Schneidezähne der Eomyiden standen zur Schmelzanalyse nicht zur Verfügung.

Longitudiale HSB ohne Umbiegung wurden bei allen überprüften Dipodidae (*Allactaga, Alactagulus, Jaculus* und *Pygeretmus*) und Zapodidae *(Sicista, Zapus)* gefunden. Hier wird zwar die relativ dicke PE wie bei den Gliroidea auch von tangentialem Schmelz gebildet, aber im Querschnitt zeichnen sich die longitudinalen HSB durch eine ganz charakteristische Fächerstellung aus (Abb. 27). Die IPM steht in einem deutlichen Winkel zu den Prismen. Diese beiden Unterschiede lassen auch diese Parallelentwicklung gut gegenüber den Gliriden abgrenzen. Die oberen Schneidezähne der Dipodidae und Zapodidae zeigen transversale HSB.

Von den Platacanthomyinen konnte nur *Typhlomys* untersucht werden. Diese Gattung besitzt in den unteren Schneidezähnen longitudinal angeordnete HSB in einer Fächerstellung. Auch hier steht die IPM im Winkel zu den Prismen. Da in dieser Gattung die PE extrem dünn ist, kann die Ausrichtung der Prismen nicht beobachtet werden. Die HSB reichen unmittelbar an die rote Außenschicht. Die oberen Schneidezähne haben transversale aber stark inklinierte HSB in der PI, und die PE mit radialem Schmelz nimmt etwa ¼ der Schmelzdicke ein.

Aus der Verbreitung von diagonal oder longitudinal ausgerichteten HSB in den Schneidezähnen myomorpher Nager geht eindeutig hervor, daß dieses Merkmal mehrfach konvergent entstanden ist. Weiter zeigt sich, daß die gleichzeitige Drehung der PI und der PE, die bei den Gliroidea belegt ist, keineswegs zwingend ist, sondern vielmehr eine Eigenart der Gliroidea bildet.

Biomechanische Bedeutung des Umbaus im Schmelzmuster

Bevor die systematische Bedeutung der Schmelzmuster erörtert werden kann, muß noch auf die biomechanische Wertigkeit der Schmelzmuster und deren Bildungsweise eingegangen werden. Die Bildung des Zahnschmelzes wird in erster Linie von genetischen und epigenetischen Faktoren gesteuert, weil im Schmelz kein struktureller Umbau, wie etwa im Knochen, möglich ist. Wenn das Schmelzmuster den biomechanischen Belastungsplan, wie z. B. in den Molaren der Arvicoliden (Koenigswald 1980, 1982), fast ideal widerspiegelt, kann das nur als Ergebnis einer sehr wirkungsvollen Selektion verstanden werden. Derartige Umkonstruktionen scheinen allerdings weniger durch Änderungen in der Nahrungsauswahl ausgelöst, sondern auf eine generelle Festigung der Struktur hin selektiert zu werden (Koenigswald und Pfretzschner 1991; Koenigswald 1989).

Da die absolute Größe bei der biomechanischen Betrachtung der Schmelzmuster eine entscheidende Rolle spielt, können die Argumente, die für die dicken, vertikal zur Kaufläche stehenden HSB, die bei Nashörnern gefunden wurden (Rensberger und Koenigs-

wald 1980; Boyde und Fortelius 1986; Pfretzschner 1992), nicht auf die uniserialen HSB der Nagezähne der Gliroidea übertragen werden.

Bisher haben sich für die Umorientierung der HSB in den Schneidezähnen verschiedener Nagetiergruppen keine biomechanischen Argumente im Sinne einer speziellen Leistungssteigerung für die unteren Schneidezähne ergeben. Besonders harte Nahrung oder eine spezielle Tätigkeit, wie etwa das Zahngraben, wird nicht von allen Gruppen geteilt, die dieses Merkmal konvergent entwickelt haben. Das Spreizen der unteren Schneidezähne belastet diese Zähne seitlich auf Biegung. Bei *Spalax* könnte man einen Zusammenhang zwischen diesem Spreizen und longitudinalen HSB vermuten, wenn nicht *Sciurus*, für den dieses Spreizen besonders gut bekannt ist, die ursprüngliche, transversale Orientierung der HSB beibehalten hätte. An funktionslose Veränderungen möchte ich bei der bei verschiedenen Nagetieren festgestellten Umorientierung der HSB nicht denken, weil regelmäßig nur die Schmelzmuster der unteren Schneidezähne nicht aber die oberen umgebaut werden. Auf einen Lösungsvorschlag für dieses Problem muß vorerst verzichtet werden.

Vergleich der bisherigen systematischen Gliederung innerhalb der Gliroidea mit den nach dem Schmelzmuster zu unterscheidenden Gruppen

Während sich die systematische Gliederung der rezenten Gliroidea auf eine Vielzahl von allgemeinen Merkmalen, auf die geographische Verbreitung und auf Weichteile (Kratochvil 1973) beziehen kann, stützt sich die Gliederung der fossilen Gliroidea bis jetzt im wesentlichen auf die Morphologie der Molaren. Die Analyse der Molarenmorphologie hat bisher kein einheitliches System erbracht.

Chaline und Mein (1979) haben eine Stammbaumrekonstruktion der fossilen und einiger rezenter Gliriden gegeben. Die drei Gruppen der vorliegenden Untersuchung werden zwar nicht ausgewiesen, lassen sich aber teilweise in der Gruppierung wiedererkennen. Die engeren Beziehungen zwischen *Microdyromys, Hypnomys, Eliomys,* und *Dryomys* innerhalb der Gruppe 2 und zwischen *Miodyromys* und *Myomimus* für die Gruppe 3 werden bestätigt. Die hier ausgewiesene Gruppe 1 wird aber auseinandergerissen und *Leithia* noch mit *Myoxus* in Verbindung gebracht. Die meisten Beziehungen lassen sich aber nicht überprüfen, weil die Schmelzanalysen vieler fossiler Gattungen noch ausstehen.

Bruijn (1967) hat eine Gliederung der Gliridae in fünf Unterfamilien gegeben, die von Daams (1981) revidiert wurde. Diese Gliederung steht in deutlichem Widerspruch zu der Gruppierung nach dem Schmelzmuster der unteren Inzisiven. Widersprüche ergeben sich aber auch zu den von Kratochvil (1973) und Bugge (1985) gegebenen zoologischen Daten.

Mayr (1979) hat bei fossilen Gliriden 6 Gruppen nach der Molarenmorphologie unterschieden, die von Meulen und Bruijn (1982) modifiziert und ergänzt wurden. Sie sind aber nicht mit den Unterfamilien bei Daams (1981) in Übereinstimmung zu bringen. Aus den sechs Morphotyp-Gruppen (Meulen und Bruijn 1982; Thenius 1989) konnten zwar jeweils einzelne Vertreter untersucht werden, aber da das Spektrum der fossilen Gattungen damit noch nicht hinreichend abgedeckt ist, muß die Bewertung der bisher sichtbaren Übereinstimmung zwischen Schmelzmuster-Gruppen und Morphotyp-Gruppen als vorläufig betrachtet werden. Sie wird so weit wie möglich diskutiert.

Kratochvil (1973) hat die am stärksten differenzierte systematische Gliederung für die rezenten Gliriden des europäischen Raumes aufgrund der Analyse der männlichen Sexualorgane gegeben. Seine Ergebnisse zeigen eine ungewöhnlich gute Übereinstimmung mit dem Schmelzmuster. Wo es Kratochvil (1973) nicht möglich war, die Sexualorgane zu untersuchen, hat er Verwandtschaftsverhältnisse aus der Molarenmorphologie rekonstruiert. Dort kommt es teilweise zu größeren Widersprüchen, die diskutiert werden müssen.

Die Gruppe 1 nach dem Schmelzmuster umfaßt *Myoxus* und *Glirulus.* Beide Gattungen

stehen bei Meulen und Bruijn (1982) in der „symmetrical group" zusammen. Allerdings wird *Glirulus* auch in einer zweiten Morphotyp-Gruppe genannt. Kratochvil (1973) betrachtet die rezenten *Myoxus* und *Glirulus* wegen der Molarenstruktur als nahestehend. Die Sexualorgane beider Gattungen wurden leider noch nicht miteinander verglichen. Bei Daams (1981) stehen diese beiden Gattungen in unterschiedlichen Unterfamilien, die jeweils Gattungen aus mehreren Schmelzmustergruppen vereinigen.

Die Gruppe 2, die sich nach dem Schmelzmuster abgrenzen läßt, umfaßt in der rezenten Fauna die Gattungen *Dryomys* und *Eliomys.* Kratovchvil (1973) vereingt sie im Tribus Dryomyini und grenzt sie aufgrund der Sexualorgane gegenüber *Myoxus* im Tribus Glirini ab. *Dryomys* und *Eliomys* bilden bei Bruijn (1966) und Daams (1981) die Dryomyinae. Engesser (1976) leitet *Tyrrhenoglis* von *Microdyromys* her. Zumindest zeigen beide das gleiche Schmelzmuster. Zammit Maempel und Bruijn (1982) werten die mediterranen Inselformen des Pleistozäns *Maltamys, Tyrrhenoglis* und *Hypnomys* als Untergattungen von *Eliomys* und stellen auch *Leithia,* die Riesenform unter den pleistozänen Gliriden aus Malta, zu den Dryomyinae. Meulen und Bruijn (1982) ordnen auch *Microdyromys* der „simple intermediate" Morphotyp-Gruppe zu. Die Übereinstimmung der Schmelzmuster dieser Gattungen in der Gruppe 2 bestätigt ihre Zusammengehörigkeit eindrucksvoll. Damit sind die früher vermuteten engeren Beziehungen zwischen *Leithia* und *Muscardinus* (Kretzoi 1943) oder zwischen *Leithia* und *Myoxus* (Chaline und Mein 1979) überholt.

Mit *„Peridyromys" brailloni* ist das Schmelzmuster der Gruppe 2 seit dem frühen Mittel-Miozän (MN4) belegt. Nach der Molarenform haben Meulen und Bruijn (1982) *„P." brailloni* jener „asymmetrical Group" zugeordnet, die weitgehend das Schmelzmuster der Gruppe 3 zeigen. *„P." brailloni* zeigt aber ein deutlich primitiveres Schmelzmuster als jene Gattungen. Ebenfalls unterschiedlich ist die Bewertung von *Myomimus,* den Kratochvil (1973) aufgrund der Größenverhältnisse in der Backenzahnreihe seinen Dryomyini zuordnet. Aufgrund des Schmelzes gehört *Myomimus* zur Schmelzmuster-Gruppe 3. Die Ähnlichkeit in den Zahnproportionen zu *Dryomys* bewerte ich als eine Plesiomorphie.

Die Gruppe 3 besitzt das am stärksten abgeleitete Schmelzmuster und ist mit *Myodyromys* mindestens seit dem unteren Mittelmiozän (MN4) belegt. Die Zuordnung der hierher gestellten Gattungen ist bisher oft geändert worden. *Muscardinus* und *Myoxus* wurden von Simpson (1945), Ellermann und Morrison-Scott (1951), aber auch noch von Daams (1981) als nahestehend angesehen. Dagegen betont Kratochvil (1973) aufgrund der männlichen Sexualorgane den großen Abstand von *Muscardinus* zu den übrigen rezenten Gliriden Europas. Ebenso weist der Besitz eines zweikammerigen Magens *Muscardinus eine Sonderstellung zu* (Vorontzov 1967). Nach Bugge (1985) hat *Muscardinus* eine stark abgeleitete Anordnung der Aorten in der Ohrregion. Die Unterschiede im Schmelzmuster zwischen der Gruppe 1 und Gruppe 3 bestätigen diesen Abstand.

Die Gruppe 3 zeigt in anderen Merkmalen eine große Divergenz, weswegen die rezenten Gattungen *Muscardinus, Graphiurus, Myomimus* alle als Vertreter eigener Unterfamilien bzw. *Selevinia* sogar als eigene Familie gewertet wurden. *Miodyromys* und *Graphiurus* haben eine einfache Molarenform beibehalten, *Muscardinus* hat die ersten Molaren vergrößert, *Selevinia* dagegen die Molaren erheblich reduziert. In der Anordnung der Aorten steht den primitiven Verhältnissen bei *Graphiurus* ein abgeleitetes Muster bei *Muscardinus* gegenüber (Bugge 1985). Dennoch teilen alle Gattungen ein stark abgeleitetes Schmelzmuster, das seit dem mittleren Miozän (MN4) belegt ist. Offensichtlich sind die verschiedenen Merkmale nicht gleichzeitig entwickelt worden, und nach dem Fossilbericht ist die Ausbildung des Schmelzmusters relativ früh erfolgt.

Selevinia wurde zwar stets in die Nähe der Gliridae gestellt, aber nie in Vergleichsuntersuchungen einbezogen. Die Übereinstimmung im Schmelzmuster, die nach der oben diskutierten Merkmalsverteilung bei den Myomorpha nicht als Konvergenz anzusehen ist, zeigt die Zugehörigkeit von *Selevinia* zur Gruppe 3 der Gliriden. Dabei wird deutlich, daß

Gliroidea

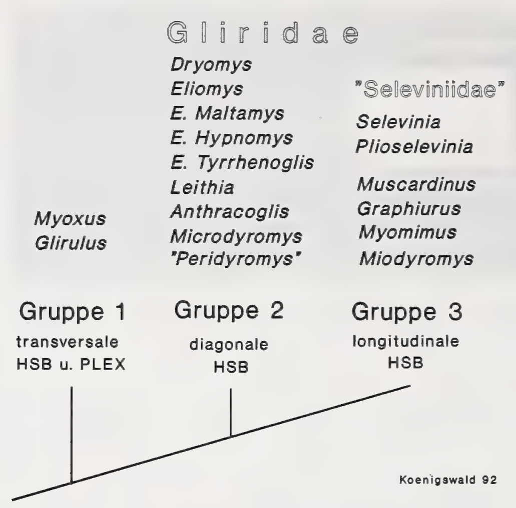


Abb. 29. Systematische Gruppierung der Gliroidea nach dem Schmelzmuster der unteren Schneidezähne. Nach diesem Merkmalskomplex sind die Seleviniidae Teil der Gliridae, weil sie nicht die Schwestergruppe aller Gliridae sind, sondern einen Teil der Schmelzmuster-Gruppe 3 bilden. Das abgeleitee Schmelzmuster der Gruppe 3 ist mit *Miodyromys* mindestens seit dem mittleren Miozän belegt, woraus sich die starke Differenzierung im Backenzahngebiß und anderen Merkmalen innerhalb dieser Gruppe erklärt

die Seleviniidae nicht die Schwestergruppe aller Gliridae sind, sondern wahrscheinlich nur eine oder wenige Gattungen innerhalb der Gruppe 3.

Die Beziehung zwischen *Selevinia* und *Plioselevinia,* die Sulimski (1962) wegen der Reduktion der Molaren angenommen hat, wird durch die Zugehörigkeit beider Gattungen zur Gruppe 3 in gewisser Weise bestätigt, aber nach dem Schmelzmuster allein wären Beziehungen zu den anderen Vertretern der Gruppe 3, etwa *Myomimus* nicht auszuschließen. Die starke Reduktion der PE bei *Plioselevinia* schließt diese Gattung aber als direkte Stammform von *Selevinia* aus.

Die drei nach dem Schmelzmuster ausgeschiedenen Gruppen dürften einheitliche Gruppen bilden, haben allerdings wegen ihres hohen Alters eine starke Differenzierung sowohl in Molaren wie in den Weichteilen erfahren. Für eine weitere Aufgliederung der Gruppen scheint das Schmelzmuster kaum geeignet zu sein. Hier leisten andere Merkmale bessere Dienste.

Taxonomische Folgerungen

Da das Schmelzmuster nicht als unmittelbare Anpassung an eine spezielle Ernährungs- oder Lebensweise zu verstehen ist, kann diesem Merkmalskomplex eine hohe systematische Signifikanz beigemessen werden. Zumindest scheint das Schmelzmuster besser mit den Weichteil-Merkmalen (Kratochvil 1973; Bugge 1985) zu korrelieren als mit den verschiedenen Systematiken, die aus der Molarenmorphologie abgeleitet worden sind (Daams 1981). Die Schmelzanalyse bietet sicherlich keine grundsätzlich besseren Merkmale als die traditionell genutzten. Sie bietet aber zusätzliche und vor allem von den bisherigen unabhängige Indizien, die in gleicher Weise und relativ einfach an fossilem wie rezentem Material überprüft werden können.

Bei den Gliroidea zeigt die hier aufgezeigte Gliederung in drei Gruppen vor allem

Probleme in der hierarchischen Bewertung der einzelnen Taxa auf. Um einen einigermaßen gleichwertigen Rang der verschiedenen Evolutionslinien auch in der Taxonomie darzustellen, könnte man alle drei nach dem Schmelzmuster ausgewiesenen Gruppen in den Rang von Unterfamilien in den Gliridae oder Familien innerhalb der Gliroidea erheben. Die Schmelzmustergruppe 1 deckt sich mit den Glirini (KRATOCHVIL 1973) nicht aber den Glirinae (THOMAS 1897). Die Gruppe 2 umfaßt weitgehend die Dryomyinae (BRUIJN 1967). Besondere Schwierigkeiten bietet die Schmelzmustergruppe 3, weil sie bereits mehrere Unterfamilien (Muscardininae, Graphiurinae, Myomiminae) und sogar die Seleviniidae als eigene Familie umfaßt.

Auf jeden Fall verlieren nach der jetzt bekannten Merkmalsverteilung die Seleviniidae den Rang einer eigenen Familie, weil sie nach dem Schmelzmuster nicht die Schwestergruppe aller Gliriden sind, sondern die einer oder mehrerer Gattungen innerhalb der Schmelzmustergruppe 3.

Die Schwierigkeit besteht darin, einerseits die traditionelle Systematik des besseren allgemeinen Verständnisses wegen soweit wie möglich beizubehalten, andererseits die hier vorgelegten Ergebnisse sinnvoll einzuarbeiten. Ich beschränke mich darauf, hier die untersuchten Gattungen entsprechend der Entwicklung im Schmelzmuster zu gruppieren (Abb. 29).

Die formale Benennung der Gruppen wäre eine rein technische Konsequenz. Bevor man sie verbindlich durchführt, sollte man aber versuchen, das Schmelzmuster von möglichst allen fossil bekannten Gliroidea zu erfassen und die Analyse der kritischen Weichteilmerkmale zu ergänzen, um zu überprüfen, wie weit die hier entworfene Hypothese einer neuen Gliederung bestätigt wird.

Danksagung

Diese Arbeit am Zahnschmelz der Gliriden war nur durch das großzügige Entgegenkommen verschiedener Kollegen möglich, die Material für die Untersuchungen zur Verfügung gestellt haben. Besonders zu nennen sind: Prof. Dr. H. DE BRUIJN, Utrecht; Dr. F. DIETERLEN, Stuttgart; Dr. B. ENGESSER, Basel; Prof. Dr. V. FAHLBUSCH, München; Prof. Dr. J. L. HARTENBERGER, Montpellier; Dr. KAWAMURA, Kariya und Mr. MINATO, Higashimurogun, Japan; Prof. Dr. J. NIETHAMMER, Bonn; Dr. O. L. ROSSOLIMO, Moskau; Dr. G. STORCH, Frankfurt, Frau Dr. WU, Peking/München. Bewährte Unterstützung fand ich bei Herrn G. OLESCHINKI und Frau D. KRANZ, beide Bonn, bei den Arbeiten für die Abbildungen. Allen sei hiermit nochmals herzlicher Dank gesagt.

Zusammenfassung

Untersucht wurde die Ultrastruktur des Schmelzes der Schneidezähne von etwa 20 rezenten und fossilen Gattungen und Untergattungen der Gliroidea. Drei Gruppen lassen sich nach dem Schmelzmuster der unteren Schneidezähne ausgliedern. Die Gruppe 1 zeigt mit vorwiegend transversalen HSB ein weitgehend ursprüngliches Schmelzmuster, besitzt aber mit der dicken PLEX eine Synapomorphie. Die umfaßt die Gattungen *Myoxus* und *Glirulus.* Die Gruppe 2 besitzt durchgehend diagonal angeordnete HSB und damit ein stärker abgeleitetes Schmelzmuster. Die Gattungen *Dryomys, Eliomys* mit mehreren fossilen Untergattungen von den Mittelmeerinseln sowie *Leithia, Microdyromys* und *„Peridyromys" brailloni* gehören zu dieser Gruppe. Sie deckt sich damit weitgehend mit den Dryomyinae. Die Gruppe 3 vereinigt durch synapomorphe Merkmale, nämlich longitudinal ausgerichtete HSB zusammen mit tangentialem Schmelz die Gattungen *Myomimus, Miodyromys, Graphiurus, Muscardinus, Plioselevinia* und *Selevinia* innerhalb des untersuchten Materials. Diese Schmelzmuster-Gruppe 3 faßt einige Gliridae und die Seleviniidae zusammen und zeigt, daß die Seleviniidae, die bisher als eigene Familie gewertet wurden, nicht die Schwestergruppe aller Gliridae sind und deswegen in die Gliridae einzugliedern sind. Das stark abgeleitete Schmelzmuster der dritten Gruppe ist bereits bei *Myodyromys* im frühen Mittel-Miozän belegt und zeigt das hohe Alter der Entwicklungs-Linien innerhalb der Gliridae. Die Gliederung nach der Feinstruktur des Schmelzes widerspricht teilweise der systematischen Gliederung nach der Molaren-Morphologie (DAAMS 1981), aber deckt sich weitgehend mit den Ergebnissen, die KRATOCHVIL (1973) aufgrund der Analyse von Weichteilen gewinnen konnte. Die Studie unterstreicht die Bedeutung der Schmelzanalyse.

Literatur

Boyde, A. (1978): Development of the structure of the enamel of the incisor teeth in the three classical subordinal groups of the rodentia. In: Development, Function and Evolution of Teeth. Ed. by P. M. Butler and K. A. Josey. London, New York, San Francisco. pp. 43–58.

Boyde, A.; Fortelius, M. (1986): Development, structure and function of rhinoceros enamel. Zool. J. Linnean Soc. **87,** 181–214.

Boyde, A.; Martin, L. (1984): A non-destructive survey of prism packing patterns in primate enamels. Amsterdam: Elsevier Science Publishers B.V. pp. 417–421.

Bruijn, H. de (1966): On the Pleistocene Gliridae (Mammalia, Rodentia) from Malta and Mallorca. Kon. Ned. Akad. Wetensch. Proc. B. **69,** 481–496.

— (1967): Gliridae, Sciuridae y Eomyidae (Rodentia, Mammalia) miocenos de Calatayud (Provincia de Zaragoza, Espana) y su relación con la bioestratigrafia del área. Bol. Inst. Geol. y Min. Madrid **78,** 188–265.

Bugge, J. (1985): Systematic value of the carotid arterial pattern in rodents. In: Evolutionary relationships among rodents: A multidisciplinary analysis. Ed. by W. P. Luckett und J. L. Hartenberger. New York: Plenum Press. pp. 355–379.

Chaline, J.; Mein, P. (1979): Les Rongeurs et l'évolution. Paris: Doin.

Daams, R. (1981): The dental pattern of the dormice *Dryomys, Myomimus, Microdyromys,* and *Peridyromys.* Utrecht Micropal. Bul. sp. publ. **3,** 1–115.

— (1990): Hypsodont Myomiminae (Gliridae, Rodentia) from the Miocene and Oligocene-Miocene boundary interval of Spain. Scripta geol. (Leiden) **95,** 1–63.

Engesser, B. (1976): *Tyrrhenoglis majori,* ein neuer fossiler Gliride (Rodentia, Mammalia) aus Sardinien. Eclogae geol. Helv. **69,** 783–793.

Ellermann, J. R.; Morrison-Scott, T. C. S. (1951): Checklist of Palaearctic and Indian Mammals 1758–1946. London: British Museum. Nat. Hist.

Hartenberger, J. L. (1971): Contribution à l'étude des genres *Microparamys* et *Gliravus* (Rodentia) de l'Eocène d'Europe. Palaeovertebrata **4,** 97–137.

Honacki, J. H.; Kinman, K. E.; Koeppl, J. W. (1982): Mammal species of the world. Lawrence: Allen Press.

Koenigswald, W. v. (1977): *Mimomys* cf. *reidi* aus der villafranchischen Spaltenfüllung Schambach bei Treuchtlingen. Mitt. Bayer. Staatsslg. Paläont. hist. Geol. **17,** 197–212.

— (1980): Schmelzmuster und Morphologie in den Molaren der Arvicolidae (Rodentia). Abh. Senckenb. naturf. Ges. **539,** 1–129.

— (1988): Enamel modification in enlarged front teeth among mammals and the various possible reinforcement of the enamel. In: Teeth revisited: Proceedings of the VIth international symposium on dental morphology. Ed. by D. E. Russell, J. P. Santoro, and D. Sigogneau-Russell. Mém. Mus. natn. Hist. nat. (C) **53,** 148–165.

— (1989): Zahnschmelz, ein natürlicher Verbundwerkstoff auf dem Prüfstand der Evolution. In: Verbundwerkstoffe und Stoffverbunde in Technik und Medizin. Bd. 2: Medizin. Hrsg. von G. Ondracek. pp. 33–48.

— (1990): Ein ungewöhnliches Schmelzmuster in den Schneidezähnen von *Marmota* (Rodentia, Mammalia). N. Jb. Geol. Paläont. Abh. **190,** 53–73.

— (1992): Tooth enamel of cave bear *(Ursus spelaeus)* and the relationship between diet and enamel structures. Ann. Zool. Fennici **28,** 217–227.

Koenigswald, W. v.; Clemens, W. A. (1992): Levels of complexity in the microstructure of mammalian enamel and their application in studies of systematics. Scanning Microscopy **6**/1, 195–218.

Koenigswald, W. v.; Pfretzschner, H. U. (1991): Biomechanics in the enamel of mammalian teeth. In: Constructional Morphology and Biomechanics. Ed. by N. Schmidt-Kittler and K. Vogel. Berlin, Heidelberg: Springer. pp. 113–125.

Korvenkontio, V. A. (1934): Mikroskopische Untersuchungen an Nagerincisiven unter Hinweis auf die Schmelzstruktur der Backenzähne. Ann. Zool. Soc. Zool.-Bot. Fennicae Vanamo **2,** 1–274.

Kratochvil, J. (1973): Männliche Sexualorgane und System der Gliridae (Rodentia). Acta Sci. Nat. Brno. NS **7**/12, 1–52.

Kretzoi, M. (1943): Ein neuer Muscardinide aus dem ungarischen Miozän. Földt. Közlem. **73,** 271–273.

Martin, T. (1992): Schmelzmikrostruktur in den Inzisiven von alt- und neuweltlichen hystricognathen und hystricomorphen Nagetieren. Palaeovertebrata (im Druck).

Mayr, H. (1979): Gebißmorphologische Untersuchungen an miozänen Gliriden (Mammalia, Rodentia) Süddeutschlands. Diss. Univ. München.

Meulen, A. van der; Bruijn, H. de (1982): The mammals from the Lower Miocene of Aliveri (Island of Evia, Greece). Part 2. The Gliridae. Kon. Ned. Akad. Wetensch. Proc. B **85**/4, 485–524.

Pfretzschner, H. U. (1992): Biomechanik der Schmelzmikrostruktur in den Backenzähnen von Großsäugern. Palaeontographica (im Druck).

Rensberger, J. M.; Koenigswald, W. v. (1980): Functional and phylogenetic interpretation of enamel microstructure in rhinoceroses. Paleobiology **6**/4, 477–495.

Simpson, G. G. (1945): The principles of classification and a classification of Mammals. Bull. Amer. Mus. Nat. Hist. **85**, 1–350.

Sulimski, A. (1962): Two new rodents from Weze 1 (Poland). Acta Palaeont. Polonica **7**, 503–512.

— (1964): Pleistocene Lagomorpha and Rodentia from Weze 1 (Poland). Acta Palaeont. Polonica **9**, 149–261.

Thenius, H. (1989): Zähne und Gebisse der Säugetiere. In: Handbuch der Zoologie. Hrsg. von J. Niethammer, H. Schliemann und D. Starck. Berlin: W. d. Guyter. Bd. VII/56, 1–513.

Tomes, J. (1850): On the structure of the dental tissue of the order Rodentia. Phil. Trans. Roy. Soc. **1850**, 529–567.

Vorontzov, N. N. (1967): Evolution of the alimentary system of myomorph rodents. Acad. Sci. USSR 1–239.

Wahlert, J. H. (1968): Variability of rodent incisor enamel as viewed in thin section, and the microstructure of the enamel in fossil and recent rodent groups. Breviora, Museum Comp. Zool. **309**, 1–18.

Wahlert, J. H.; Koenigswald, W. v. (1985): Specialized enamel in incisors of eomyid rodents. Amer. Mus. Novitates **2832**, 1–12.

Zammit Maempel, G.; Bruijn, H. de (1982): The Plio/Pleistocene Gliridae from the Mediterranean Islands reconsidered. Proc. Kon. Ned. Akad. wetensch. B **85**/1, 1113–128.

Anschrift des Verfassers: Prof. Dr. Wighart v. Koenigswald, Institut für Paläontologie, Universität Bonn, Nußallee 8, D-5300 Bonn 1, Deutschland

Z. Säugetierkunde 58 (1993) 116–121

ISSN 0044-3468

Effect of removing the chin gland on chin-marking behaviour in male rabbits of the New Zealand race

By Rosario Chirino, Gabriela González-Mariscal, P. Carrillo, P. Pacheco, and Robyn Hudson

Centro de Investigación en Reproducción Animal, Universidad Autónoma de Tlaxcala-CINVESTAV; Instituto de Neuro-Etología, Universidad Veracruzana; Instituto de Investigaciones Biomédicas, Universidad Nacional Autónoma de México, México, and Institut für Medizinische Psychologie, Universität München, Germany

Receipt of Ms. 1. 4. 1992
Acceptance of Ms. 3. 9. 1992

Abstract

In male domestic rabbits the effect of removing the chin gland on the performance of chin-marking behaviour was examined and compared with the known effects of castration. The marking frequency of eight intact adult bucks was recorded for a 4-week baseline period after which the chin gland was excised. Testing was resumed two days later for a further 4, 18 or 30 weeks. Four animals were also castrated either 4 or 18 weeks after gland removal. They were then tested for a further 10 weeks without treatment, for 16 days during administration of testosterone propionate (TP), and for 2 weeks following TP withdrawal. Chinning declined by 24 % within two months of gland removal in gonadally intact animals, and castration reduced this behaviour by more than half again within a month. TP administration stimulated chinning while TP withdrawal resulted in a return to pre-treatment values within a week. Thus, while the chin gland and/or its secretions may modulate chin marking, gonadal androgens appear to have the major stimulatory function.

Introduction

Rabbits (*Oryctolagus cuniculus*) of both sexes posses a distinctive chin gland, the secretion from which they use to mark objects in their environment by rubbing their chin over them (Black-Cleworth and Verberne 1975; Hudson and Vodermayer 1992; Lyne et al. 1964; Mykytowycz 1962). In males, both the frequency of chinning and the size and secretory activity of the gland correlate positively with social rank and reproductive activity (Bell 1985; Black-Cleworth and Verberne 1975; Mykytowycz 1962, 1965, 1972, 1975; Mykytowycz and Dudzinski 1966; Mykytowycz et al. 1976), and chinning is therefore thought to be involved in territorial defence, in the establishment and maintenance of the social hierarchy and in the modulation of reproductive activity.

Testicular androgens appear to play a major role in the regulation of this behaviour. Thus, whereas castration reduces the frequency of chinning (González-Mariscal et al. 1992b; Mykytowycz 1962, 1965), the size of the gland and its histological appearance (Mykytowycz 1965; Strauss and Ebling 1970; Wales and Ebling 1971), administration of testosterone propionate reverses these effects (González-Mariscal et al. 1992b; Mykytowycz 1962; Strauss and Ebling 1970; Wales and Ebling 1971). However, as it is not known to what extent the gland itself contributes to the performance of chinning, it was the purpose of the present study to investigate the effect of removing the chin gland on the marking behaviour of adult male rabbits.

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5802-0116 $ 02.50/0

Material and methods

Animals

Eight adult New Zealand white bucks from the Tlaxcala colony, aged from 1–3 years and weighing from 3.8–4.2 kg were used. The animals were separately caged under natural light and temperature conditions (11–13 h light/day, 19 ± 3 °C), with continuous access to rabbit pellets (Conejina, Purina) and water.

Drugs

Testosterone propionate was obtained from Sigma (St. Louis, Missouri, USA).

Behavioural testing

Chin-marking activity was assessed as described previously (Hudson et al. 1990) by placing bucks individually for 15 min a day in a wire-mesh arena 1 m in diameter and 43 cm high, containing three, 15-cm high terracotta bricks arranged in a triangle, approximately 0.5 m apart. The number of times an animal rubbed its chin on the bricks or the arena walls during the test period was recorded. As we had earlier found that the use of either fresh bricks or those previously marked by familiar test animals did not modify chinning frequency of either male or female subjects (González-Mariscal et al. 1992b; Hudson and Vodermayer 1992), the same bricks were used throughout the study. Furthermore, as animals were operated successively over several months and tested in each session in random order, subjects were presented for most of the test period with bricks marked by both intact and operated animals. By staggering the operative procedures, animals in different states could be tested in parallel, and effects due to a lack of chin marks on the bricks per se rather than to the experimental procedures themselves, could thus be minimized. Observations were conducted inside the rabbit colony between 17.00–19.00 h from September 1988 to January 1990.

Experimental procedures

To allow animals to adapt to the experimental conditions they were introduced to the arena during the first week for 15 mins a day without recording chinning. After this period, chinning was recorded for a minimum of 3 and in most cases for 5 days a week under the following conditions: a. during a control period of four weeks, after which the chin gland was excised; b. starting 48 hours after surgery, gonadally intact animals were tested for a further 4 (N = 2), 18 (N = 2), or 30 weeks (N = 4) (cf. Fig. 1); c. four animals were castrated either 4 (N = 2) or 18 weeks (N = 2) after removal of the gland and tested for a further 10 weeks; d. following this period, castrated subjects were tested during 16 days of treatment with testosterone propionate (TP; 1 mg/day, s.c. in 1 ml sesame oil), and for 2 weeks after discontinuing TP treatment (cf. Fig. 2). A group of intact control animals was not included since we had earlier found that daily testing of both male and female rabbits over periods of two months or more does not lead to a reduction in chinning (González-Mariscal et al. 1992a, b; Hudson 1992).

Surgery

The chin gland has been morphologically well described and is reported to consist of several discrete glandular masses including a large superficial medial group and a smaller deep lateral group situated on either side of the lower jaw (Lyne et al. 1964; Mykytowycz 1965). To remove these glands, the animals were anesthetized using 0.7 g/kg urethane administered as a 20 % solution i.p. After depiliating the chin region, a 3 cm midline section was made and the skin retracted first to one side and then to the other so as to bilaterally remove the two groups of glands. In this study these were found to comprise two superficially located glandular masses encapsulated in connective tissue and readily removed, and a deeper lying, less accessible posterior mass. Surgery could be accomplished with little or no bleeding, and following excision of all visible glandular and associated connective tissue, the wound was sutured closed and an antiseptic spray (Pisan) applied locally. All wounds healed within a few days with no sign of infection.

Bilateral castration was also performed under urethane anesthesia and the wounds sutured closed and treated locally with antiseptic spray. The animals recovered rapidly with no apparent complications.

Statistical analysis

To analyze the effect of removing the chin gland on marking activity, mean monthly values were calculated for each of the 6 bucks remaining gonadally intact to post-operative week 18, and their monthly post-operative scores compared to the pre-operative baseline values using the nonparametric, two-tailed Wilcoxon test.

Results

During baseline testing the animals appeared to adjust rapidly to the arena and by the second week started vigorously marking as soon as they were placed in it. Although there was considerable individual variability in the frequency of chinning, with average scores ranging between 60 and 140 marks per session, group values remained relatively stable at around 105 marks per session (Fig. 1).

Gland removal

Removal of the chin gland had no immediate visible effect on the marking behaviour of any of the animals. As shown in Figure 1, chinning scores remained high throughout most of the first post-operative month, with no significant differences when compared to baseline ($N = 6$, $T = 4$, $p > 0.05$). In fact, even on the first day of testing, that is 48 h after surgery, the vigor and frequency of chinning appeared unaltered. However, during the second month following gland removal, a significant decline in chinning from the baseline average of about 105 marks/15 min to an average of 80 marks/15 min ($N = 6$, $T = 0$, $p < 0.05$) was recorded. Scores then stabilized with no significant difference found between the means of the second and third months ($N = 6$, $T = 7$, $p > 0.05$). Furthermore, the mean chinning frequency of the four animals which remained uncastrated throughout the entire experiment varied little from week 18 (66 ± 5 marks/15 min) to week 30 (79 ± 6 marks/15 min) following gland removal.

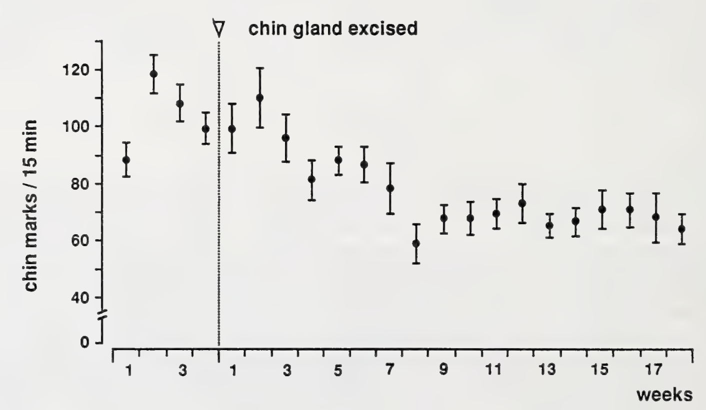


Fig. 1. Effect of removing the chin gland on the marking frequency of gonadally intact adult male rabbits. Chinning frequency was determined by placing animals in a wire-mesh arena containing three bricks, and counting the number of times animals rubbed their chin on these. Sessions lasting 15 mins were conducted three to five times a week for a four-week baseline period ($N = 8$), after which the chin glands were removed. Eight animals were tested to post-operative week 5, and six thereafter. Means and standard errors of the mean are given

Castration

Castration resulted in a clear decline in marking activity within a month (Fig. 2). This was true regardless of the time elapsing between chin-gland removal and castration. During this period, marking activity declined by an average of 50 %, after which it appeared to stabilize.

Testosterone administration

Daily administration of TP increased the average level of marking activity from 14 marks/15 min on day 1 of treatment to 52 marks/15 min by day 14 (Fig. 2). Discontinuing the treatment resulted in a return to pre-TP baseline values within a week, with scores declining from an average of 52 marks/15 min on the last day of TP treatment to 13 marks/15 min seven days later.

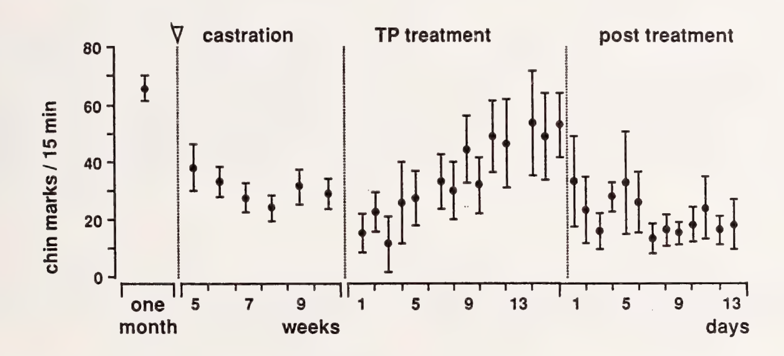


Fig. 2. Effect of castration and of androgen replacement and withdrawal on the chinning frequency of adult male rabbits following chin-gland removal. The chinning frequency of four bucks was determined in three to five, 15 minute test sessions per week under the following conditions: a. without chin glands for one month before castration; b. for ten weeks after castration; c. for 16 days with daily administration of testosterone propionate (TP; 1 mg/day); d. for 13 days after TP withdrawal. Means and standard errors of the mean are given

Discussion

The present results demonstrate that removal of the chin gland in gonadally intact male rabbits results in a significant decrease in chin-marking behaviour. However, the effect was slow, two months being required for a significant reduction in chinning frequency to occur. The fact that normal levels of marking were observed two days after surgery and throughout the following month makes it unlikely that the reduction was simply an artefact of the surgical procedure. As the chinning activity of intact male and female rabbits in the laboratory arena remains stable over months (González-Mariscal et al. 1990, 1992a, b; Hudson 1992; Hudson and Vodermayer 1992), it is also unlikely that the decrease in chinning was simply due to habituation or to a decline in general motivation. Furthermore, as animals were operated and tested throughout the year, seasonal effects can also be excluded. Thus, these data would suggest that the chin gland itself or its secretions are involved in the regulation of chinning in buck rabbits. This contrasts somewhat with the study of Blum and Thiessen (1970) who found that ventral gland excision did not modify the frequency of scent-marking in male Mongolian gerbils tested five weeks after surgery. However, while species differences are quite possible, the results of the present study suggest it may be necessary to wait as long as two or three months for the effects of gland excision to become apparent.

The mechanisms mediating the decline in marking activity following chin-gland removal are unknown. However, since removal of the gland eliminates the secretions normally deposited during chinning, the decline may have been due to the failure of animals to gain confirmation of the effectiveness of the marking act. Should such olfactory feedback indeed be important in regulating chinning, then covering the gland to prevent deposition of secretion could be expected to result in a similar decline. Nevertheless, gonadal androgens appear to be the main activators of this behaviour as chin-gland excision in gonadally intact animals resulted in only a moderate decrease in marking after a long latency.

Irrespective of the mechanisms mediating the decrease in chinning following gland removal, it is clear that this effect was not as rapid or marked as following castration. Thus, while castration has been found to reduce marking by nearly 60 % within 3–4 weeks (González-Mariscal et al. 1992b), chin-gland removal decreased chinning by only 24 % two months postoperatively.

In summary, chinning in rabbits seems to be regulated primarily by gonadal steroids. These hormones are able to stimulate chinning independently of the gland since TP stimulates marking in animals with or without chin glands, and castration reduces chinning to a similar extent in both groups. Nevertheless, the finding that chin-gland removal may also reduce the frequency of chinning suggests the regulation of this behaviour to be complex, probably involving a combination of hormonal, olfactory and somatosensory mechanisms.

Acknowledgements

This work was supported by funds provided by the Secretaria de Education Publica de México (DGICSA: C90-01-0439; to P.P.) and the Deutsche Forschungsgemeinschaft (Hu 426/1; Po 121/13).

Zusammenfassung

Der Einfluß der Entfernung der Kinndrüse auf das Kinn-Markierverhalten von männlichen Kaninchen der Neuseeland-Rasse

Bei männlichen Hauskaninchen wurde der Einfluß der Entfernung der Kinndrüse auf die Häufigkeit von Kinnmarkierverhalten untersucht und mit dem der Kastration verglichen. Das Markierverhalten von 8 Rammlern wurde vor Entfernung der Kinndrüse für die Dauer von 4 Wochen aufgezeichnet, und dann, 2 Tage nach dem Eingriff, für weitere 4, 18 oder 30 Wochen getestet. Die ersten 4 Tiere wurden danach zusätzlich kastriert und für weitere 10 Wochen auf ihre Kinnmarkieraktivität untersucht. Schließlich erhielten diese Tiere für 16 Tage 1 mg Testosteron-Proprionat (TP) pro Tag, und wurden dann weitere zwei Wochen beobachtet. Innerhalb von 2 Monaten nach Entfernung der Drüse sank die Markierhäufigkeit bei nicht-kastrierten Tieren um 24 %. Kastration führte zu einer zusätzlichen Abnahme um mehr als 50 % innerhalb eines Monats und Behandlung mit TP zu einer vorübergehenden Stimulation des Kinnmarkierverhaltens. Dies bedeutet, daß die Kinndrüse und/oder die Kinndrüsensekrete zwar modulierend wirken können, die Androgene das Markierverhalten aber am stärksten beeinflussen.

References

Bell, D. J. (1985): The rabbits and hares: order Lagomorpha. In: Social Odours in Mammals. Ed. by R. E. Brown and D. W. MacDonald. Oxford: Clarendon Press. Pp. 507–530.

Black-Cleworth, P.; Verberne, G. (1975): Scent-marking, dominance and flehmen behaviour in domestic rabbits in an artificial laboratory territory. Chem. Sens. Flav. **1**, 465–494.

Blum, S. L.; Thiessen, D. D. (1970): Effect of ventral gland excision on scent marking in the male Mongolian gerbil. J. Comp. Physiol. Psychol. **73**, 461–464.

González-Mariscal, G.; Melo, A. I.; Zavala, A.; Beyer, C. (1990): Variations in chin-marking behaviour of New Zealand female rabbits throughout the whole reproductive cycle. Physiol. Behav. **48**, 361–365.

— — — — (1992a): Chin-marking behaviour in male and female New Zealand rabbits: Onset, development and activation by steroids. Physiol. Behav. (in press).

González-Mariscal, G.; Melo, A. I.; Zavala, A.; Chirino, R.; Beyer, C. (1992b): Sex steroid regulation of chin-marking behaviour in male New Zealand rabbits. Physiol. Behav. (in press).

Hudson, R. (1992): Differential effects of exogenous melatonin on correlates of oestrus in domestic rabbits. Proc. VII Ann. Meeting Europ. Soc. Chronobiol. (in press).
Hudson, R.; Gonzalez-Mariscal, G.; Beyer, C. (1990): Chin-marking behaviour, sexual receptivity and pheromone emission in steroid treated, ovariectomized rabbits. Horm. Behav. **24**, 1–13.
Hudson, R.; Vodermayer, T. (1992): Spontaneous and odour-induced chin-marking in domestic female rabbits. Anim. Behav. **43**, 329–336.
Lyne, A. G.; Molyneux, G. S.; Mykytowycz, R.; Parakkal, P. F. (1964): The development, structure and function of the submandibular cutaneous (chin) glands in the rabbit. Aust. J. Zool. **12**, 340–348.
Mykytowycz, R. (1962): Territorial function of chin gland secretion in the rabbit, *Oryctolagus cuniculus* L. Nature **193**, 799.
— (1965): Further observations on the territorial function and histology of the submandibular cutaneous (chin) glands in the rabbit, *Oryctolagus cuniculus* L. Anim. Behav. **13**, 400–412.
— (1972): The behavioural role of the mammalian skin glands. Naturwiss. **4**, 133–139.
— (1975): Activation of territorial behaviour in the rabbit, *Oryctolagus cuniculus*, by stimulation with its own chin gland secretion. In: Olfaction and Taste V. Ed. by D. A. Denton and J. P. Coghlan. New York: Academic Press. Pp. 425–432.
Mykytowycz, R.; Dudzinski, M. L. (1966): A study of the weight of odoriferous and other glands in relation to social status and degree of sexual activity in the wild rabbit, *Oryctolagus cuniculus* (L.). CSIRO Wildl. Res. **11**, 31–47.
Mykytowycz, R. A.; Hesterman, E. R.; Gambale, S.; Dudzinski, M. L. (1976): A comparison of the effectiveness of the odors of rabbits, *Oryctolagus cuniculus*, in enhancing territorial confidence. J. Chem. Ecol. **2**, 13–24.
Strauss, J. S.; Ebling, F. J. (1970): Control and function of skin glands in mammals. Mem. Soc. Endocrinol. **18**, 341–371.
Wales, N. A. M.; Ebling, F. J. (1971): The control of the apocrine glands of the rabbit by steroid hormones. J. Endocrinol. **51**, 763–370.

Authors' addresses: Rosario Chirino, Gabriela González-Mariscal, Porfirio Carrillo and Pablo Pacheco, Centro de Investigación en Reproducción Animal, Universidad Autónoma de Tlaxcala-CINVESTAV, Apdo Postal 62, Tlaxcala, Tlax. 90 000, México; Robyn Hudson, Institut für Medizinische Psychologie, Goethestr. 31, D-8000 München 2, Germany

Z. Säugetierkunde 58 (1993) 122–123

ISSN 0044-3468

WISSENSCHAFTLICHE KURZMITTEILUNGEN

Adoptive behaviour in Fallow deer (*Cervus dama*)

By Cristina San José and F. Braza

Estación Biológica de Doñana, Sevilla, Spain

Receipt of Ms. 5. 3. 1992
Acceptance of Ms. 21. 8. 1992

In the Cervidae, occasional adoptive behaviour has been described (e.g. Altmann 1963; Woodson et al. 1980) and recently, Birgersson et al. (1991) have furnished new information about allosuckling in an enclosed population of *Cervus dama*.

During the fawning season (25 May–15 June of 1991) we observed a wild fallow deer population in Doñana National Park (SW Spain). The 20 known females present in the area were monitored with a telescope from a 30 m high tower to determine the birth date and to capture their newborn fawns.

On the 2nd of June at 10:05 h two new born fawns (female and male) were captured, sized and marked (in about 15 min) in nearby sites (approximately 100 m). Both fawns (the male being born 6 h later) weighed 5100 g. Their weights are included in the rank of those recorded for the rest of newborn fawns captured in the same area ($\overline{X}$ = 5014.6 g, SD = ±438.3 g, n = 24). On the 3rd of June the mother of the female fawn adopted the male once after this fawn was rejected by its own mother. Both fawns have been observed alive after 6 months.

The duration of suckling bout periods during the early isolation period (first 10 days of life, San José and Braza 1992) were recorded for the "twin" fawns and for the rest of marked fawns (four males and six females) in the study area in order to compare suckling behaviour of "twins" with single fawns. Two consecutive suckling bouts were considered distinct when separated by more than 5 min. Suckles lasting 5 sec or less were considered suckling attempts. The Table represents the results of the analysis. Significant differences between "twins" and single fawns were detected during the isolated period, mainly due to differences in the first five days of life. No differences between sexes were detected during this period either in "twins" or in single fawns (t-test). Some studies found that each twin sucks as often as any single fawn, the milk production rates being higher in does with twin fawns (Sadleir 1980; Gauthier and Barrette 1985).

Mean duration of suckling bouts (sec.)

Age	"Twins"			Singles			t-test		
(days)	n	$\overline{X}$	SD	n	$\overline{X}$	SD	t	df	p
1–5	29	231.7	183.7	28	91.1	50.8	3.9	55	0.0003
6–11	16	123.3	95.5	9	77.4	46.7	1.3	23	NS
1–11	45	193.2	165.3	37	87.7	49.5	3.7	80	0.0003

n = number of suckling bouts recorded, $\overline{X}$ = mean, SD = standard deviation, t = value of the Student statistic, df = degrees free, p = probability, NS = not significant.

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5802-0122 $ 02.50/0

Several hypotheses have been developed regarding possible selective benefits and environmental constraints associated with alloparental care and adoption (RIEDMAN 1982). Some of the circumstances considered in these hypotheses are present in our study population: groups of fallow deer females are constituted by members related by matrilineal descent (SAN JOSÉ 1988) and present an extraordinary attachment to particular areas (SAN JOSÉ and BRAZA 1991). A high degree of inbreeding is taking place, and a monomorphism of focused haemoglobin has been detected in the Doñana fallow deer population (SCHREIBER et al. 1992). In this case, fostering behaviour could have arisen by means of kin selection (RIEDMAN 1982). However, the case of adoption observed in our study population may also be attributed to a reproductive error on the part of the foster mother as occurs in many mammals, (revision of cases in RIEDMAN 1982). It is also interesting that last year the mother of the female fawn lost its fawn after this was marked. This female is seven years old and has given birth during the last six years. The fact that it didn't rear any fawn last year, together with the good environmental conditions in spring 1991 perhaps contributed to a particularly good physical condition of this female this year.

Although this report represents only an isolated case, it reveals that extra maternal investment is possible in fallow deer. This doesn't follow the hypotheses recently posed by BYERS and MOODIE (1990) which predicts that the level of resources that mothers must provide to support high postnatal growth rates (as in the case of ungulates) precludes any extra investment in individual sons. We think that if it is possible for a mother to make an extra investment to rear a strange male fawn, a margin probably exists in the amount of partental investment allocated by a mother to her fawn depending on different factors such as the sex of the fawn or its own physical condition. Since the food requirements could play an important role, in captivity they can cause conditions favourable for alloparental suckling behaviour to take place as has been observed by BIRGERSSON et al. (1991).

Literature

ALTMANN, M. (1963): Naturalistic studies of maternal care in moose and elk. In: Maternal Behaviour in Mammals. Ed. by H. L. RHEINFOLD. New York: Wiley. Pp. 210–225.

BIRGERSSON, B.; EKVALL, K.; TEMRIN, H. (1991): Allosuckling in fallow deer, *Dama dama*. Anim. Behav. **42**, 326–327.

BYERS, J. A.; MOODIE, J. D. (1990): Sex-specific maternal investment in pronghorn, and the question of a limit on differential provisioning in ungulates. Behav. Ecol. Sociobiol. **26**, 157–164.

GAUTHIER, D.; BARRETTE, C. (1985): Suckling and weaning in captive white-tailed and fallow deer. Behaviour **94**, 128–149.

RIEDMAN, M. L. (1982): The evolution of alloparental care and adoption in mammals and birds. Q. Rev. Biol. **57**, 405–435.

SADLEIR, R. M. (1980): Milk yield of black-tailed deer. J. Wildl. Manage. **44**, 472–478.

SAN JOSÉ, C. (1988): Estrategia reproductiva de las hembras de gamo (*Dama dama*). Tesis Doctoral, Univ. Complutense Madrid.

SAN JOSÉ, C.; BRAZA, F. (1991): An approach to management of wild populations of fallow deer (*Dama dama*) in Doñana National Park. In: Global trends in wildlife management. Ed. by B. BOBEK, K. PERZANOWSKI, and W. L. REGELIN. Kraków-Warszawa: Swiat Press.

— — (1992): Antipredator aspects of fallow deer behaviour during calving season at Doñana National Park (Spain). Ethol. Ecol. Evol. **4**, 139–149.

SCHREIBER, A.; BRAZA, F.; SAN JOSÉ, C.; ARAGON, S. (1992): Relationships of fetal haemoglobin to age of newborn fallow deer fawns, *Dama dama*. Can. J. Zool. (in press).

WOODSON, D. L.; REED, E. T.; DOWNING, R. L.; MCGUINNESS, B. S. (1980): Effect of fall on planning on white-tailed deer fawns and yearlings. J. Wildl. Manage. **44**, 249–252.

Authors' address: Dra. CRISTINA SAN JOSÉ and Dr. FRANCISCO BRAZA, Estación Biológica de Doñana, Apdo. 1056, E-41080 Sevilla, Spain

Z. Säugetierkunde 58 (1993) 124–126

ISSN 0044-3468

Relative growth of sexual organs in males of *Arvicola terrestris* (Rodentia, Arvicolidae) from the Iberian Peninsula

By J. Ventura

Departamento de Biología Animal (Vertebrados), Universidad de Barcelona, Spain

Receipt of Ms. 2. 7. 1992
Acceptance of Ms. 13. 11. 1992

In recent studies (Ventura 1988; Ventura and Gosálbez 1990a, b) the reproductive characteristics of the northern water vole, *Arvicola terrestris*, in the Spanish Pyrenees were determined. The breeding season of this population starts in March and ends in October–November. Clearly related with the reproductive cycle, the testis and the seminal vesicle of adult individuals show a noticeable variation in size during the year. The minimum size is reached in December and the maximum between April and June (Ventura and Gosálbez 1990a). With the aim of discribing the reproductive dynamics of the species in this area more precisely, the relative growth of the testis and the seminal vesicle, according to the time of the year, are reported in this study.

The analysed sample included 273 males obtained by monthly captures between 1983 and 1984 in the Aran Valley (Lérida, Spain). The animals were collected after death and subsequently dissected to study their sexual condition. Head-body lengths (HBL, mm) and body weights (BW, g) were taken. The size of the testis and the seminal vesicle was estimated by measuring their maximum lengths (Gosálbez and Sans-Coma 1976; Heske and Ostfeld 1990). The specimens were distributed into six classes of relative age according to the criteria outlined by Ventura and Gosálbez (1990a). Taking into account the reproductive cycle and the structure of this population throughout the year (Ventura et al. 1991), 98 males were selected in order to analyse the growth patterns of the sex organs considered. The samples were distributed into two groups according to the month of capture: April– July (class 0, $n = 2$; class I, $n = 10$; class II, $n = 12$; class III, $n = 8$; class IV, $n = 9$; class V, $n = 12$); October–February (class I, $n = 7$; class II, $n = 9$; class III, $n = 11$; class IV, $n = 11$; class V, $n = 7$). With the logarithmic values of the data, regressions were calculated using the geometric mean method (see Ricker 1973; Sokal and Rohlf 1981). The significance of the differences between two regression coefficients was determined by the comparison of their confidence limits at 95 % probability (Sokal and Rohlf 1981).

The correlation between the testis length (TL, in mm) and the seminal vesicle length (VL, in mm) corresponding to the specimens of classes I–IV captured between April and July shows a positive allometry favourable to VL ($\log VL = -0.9878 + 2.1029 \log TL$, $r = 0.9$). In the relationship of BW to TL and VL in the specimens of age classes I–IV (Fig. 1a), BW is used as an estimate of age (Ventura and Gosálbez 1990a). The correlation coefficients obtained during April–July are clearly significant (always $r = 0.9$, $p < 0.001$). The confidence limits of the slopes reveal significant differences between both regression lines, so that while VL shows a positive allometric increase to BW ($\log VL = -3.0234 + 2.0115 \log BW$), TL shows a slight negative allometry to the latter ($\log TL = -0.9730 + 0.9584 \log BW$). The projection of the intersection point of both regression lines over the abcissa may be considered as an estimate of the body weight at which the length inversion between the testis and the seminal vesicle occurs. The value obtained in April–July is (Fig. 1a): $x_1 = 1.9470$; antilog $x_1 = 88.5$ g.

The correlation between TL and VL in the specimens of age classes I–IV captured in

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5802-0124 $ 02.50/0

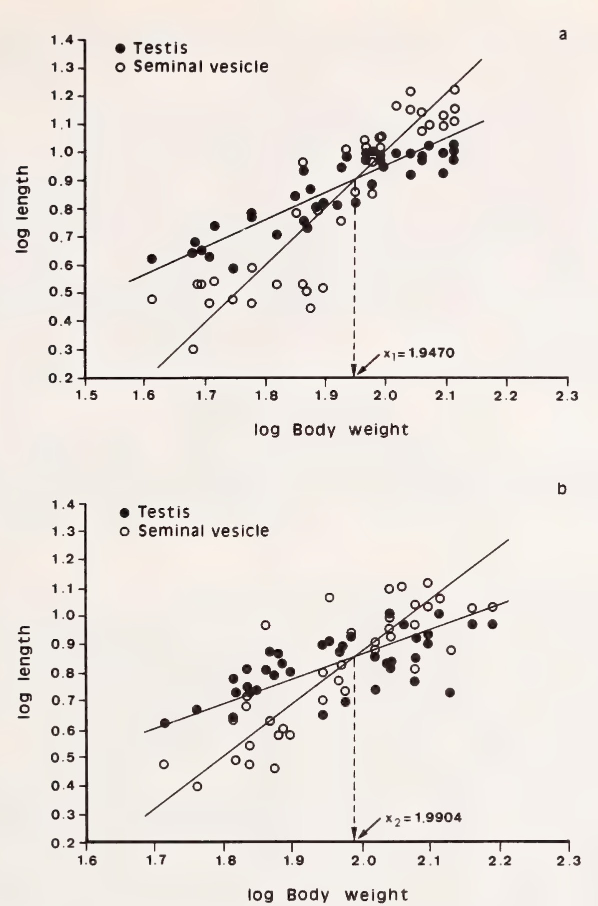


Fig. 1. Graphs on logarithmic coordinates of the relationships considered in *Arvicola terrestris* during April–July (a) and October–February (b)

October–February reveals a positive allometry favourable to VL (log VL = −0.9665 + 2.1362 log TL, r = 0.74), showing a regression coefficient similar to that observed during April–July. The plot of BW against TL and VL during October–February in the specimens of classes I–IV (Fig. 1b) coincides with the patterns obtained in spring-summer, but the correlation coefficients are clearly lower in the former period (log TL = −0.8603 + 0.8595 log BW, r = 0.65; log VL = −2.8034 + 1.8362 log BW, r = 0.85). The projection over the abcissa of the intersection point between both regression lines gives (Fig. 1b): x_2 = 1.9904; antilog x_2 = 97.8 g.

The regression equations show that, independent of the season, the seminal vesicle exhibits a positive allometric increase in relation to the testis. Taking into account the age classes, the length inversion between both organs occurs in the II–III transition (Ventura 1988). In this population this interval corresponds to the period in which males reach sexual maturity (Ventura and Gosálbez 1990a). The value of 88.5 g obtained in the plot of BW against TL and VL in April–July falls within the range given by Ventura and Gosálbez (1990a) for this phenomenon.

As has been reported in other rodent species (Breakey 1963; Martinet 1972; Vargas et al. 1984) the testes grow slowly during winter. Likewise, due to the physiological

relationship between the testes and the sex accessory organs (Hogarth 1978; Bronson 1989), the seminal vesicle also exhibits similar growth patterns. The higher estimate for body weight obtained in October–February indicates a greater and faster growth of the testis and the seminal vesicle during April–July.

According to these results in *A. terrestris* from the Iberian Peninsula the existence of a decrease in testis (and seminal vesicle) growth rhythm during the sexual-resting period can be deduced. Probably, this phenomenon is accompanied by a delay in the onset of sexual maturity in the animals born at the end of summer and the beginning of autumn. This may consequently explain the presence of some submature animals of class III during October–December (Ventura and Gosálbez 1990a). Future physiological studies are needed to confirm these observations, and to determine the extent of the delay in the onset of sexual maturity in individuals born at the end of the breeding season.

Acknowledgements

The author is grateful to J. Gosálbez for his comments on this study. Thanks are also due to M. Marqués, S. Ruiz, S. Lluch and G. Jordán for their helpful assistance in the field work.

References

Breakey, D. R. (1963): The breeding season and age structure of feral house mouse populations near San Francisco Bay, California. J. Mammalogy **44**, 153–167.
Bronson, F. H. (1989): Mammalian reproductive biology. Chicago: University Chicago Press.
Gosálbez, J.; Sans-Coma, V. (1976): Sobre el topillo rojo, *Clethrionomys glareolus* Schreber, 1780, en la región del Montseny (Catalunya, España). Säugetierkdl. Mitt. **24**, 77–79.
Heske, E. J.; Ostfeld, R. S. (1990): Sexual dimorphism in size, relative size of testes, and mating systems in North American voles. J. Mammalogy **71**, 510–519.
Hogarth, P. J. (1978): Biology of reproduction. Glasgow: Blackie.
Martinet, L. (1972): Recherches sur les causes de les variations des populations du Campagnol des champs *Microtus arvalis*. PhD Diss., Univ. Paris VI.
Ricker, W. E. (1973): Linear regressions in fishery research. J. Fish. Res. Board Can. **30**, 409–434.
Sokal, R. R.; Rohlf, F. J. (1981): Biometry: the principles and practice of statistics in biological research. (2nd ed.). San Francisco: W. H. Freeman.
Vargas, J. M.; España, M.; Palomo, L. J.; Sans-Coma, V. (1984): Über die Geschlechtstätigkeit der *Mus spretus*-♂♂ in Südspanien. Z. angew. Zool. **71**, 257–273.
Ventura, J. (1988): Contribución al conocimiento del género *Arvicola* Lacépède, 1799, en el nordeste de la Península Ibérica. PhD Diss., Univ. Barcelona.
Ventura, J.; Gosálbez, J. (1990a): Reproductive cycle of *Arvicola terrestris* (Rodentia, Arvicolidae) in the northeast of the Iberian Peninsula. Z. Säugetierkunde **55**, 383–391.
— (1990b): Reproduction potential of *Arvicola terrestris* (Mammalia, Rodentia) in the northeast of the Iberian Peninsula. Zool. Anz. **224**, 45–54.
Ventura, J.; Gosálbez, J.; López-Fuster, M. J. (1991): Structure de population d'*Arvicola terrestris* (Linnaeus, 1758) du nord-est ibérique. Mammalia **55**, 85–90.

Author's address: Dr. Jacint Ventura, Departamento de Biología Animal (Vertebrados), Facultad de Biología, Avda. Diagonal, 645, E-08028 Barcelona, Spain

Ankündigung der 126. Jahresversammlung der Deutschen Ornithologen-Gesellschaft 1993

Die 126. Jahresversammlung der Deutschen Ornithologen-Gesellschaft findet auf Einladung des Vereins Sächsischer Ornithologen in Meerane bei Chemnitz von Mittwoch, 8. September (Anreisetag) bis Sonntag, 12. September 1993 statt.

Das Vortragsprogramm steht unter den Hauptthemen: „Vögel in der Zivilisationslandschaft“ und „Sinnesphysiologie“.

Beiträge namhafter osteuropäischer Ornithologen werden das Programm bereichern.

Fragen zum Tagungsprogramm sind zu richten an den Generalsekretär der Deutschen Ornithologen-Gesellschaft, PD Dr. Erich Glück, Lehrstuhl für Landschaftsökologie, Olshausenstr. 40, W-2300 Kiel 1, Tel. (04 31) 8 80-41 21.

Für die Quartierbestellung und örtliche Tagungsangelegenheiten ist der Geschäftsführer des Vereins Sächsischer Ornithologen, Herr Hartmut Meyer, Postfach 29, O-9270 Hohenstein-Ernstthal, Tel. (07 23) 21 07, Fax (07 23) 21 08, zuständig.

PALMEIRIM, J. M.: **Bats of Portugal: Zoogeography and Systematics.** Lawrence: The University of Kansas, Museum of Natural History, 1990. Miscellaneous Publication No. 82. 53 pp., 39 figs., 24 tabs. ISBN 0-89338-034-2

The goals of this review are 1. to compile all available published information on continental Portuguese bats (not Madeira or Azores), 2. to summarize the considerable number of recent distributional records, 3. to discuss the patterns of distribution within Iberia (and western Palearctic region), 4. to analyse the taxonomic status of 21 species, and 5. to provide morphological descriptions and keys for identification. A dose similarity amongst the Portuguese and other European bat populations is shown. No endemic Iberian subspecies could be recognized. The Iberian bat fauna is dominated by Palearctic species and has a Mediterranean-Atlantic character. The most common pattern of distribution is that shown by species present throughout most of the Iberian Peninsula; a second pattern comprises southern species that do not reach northern Iberia, and a third pattern is shown by species that do not reach the southern part of the Peninsula. E. KULZER Tübingen

MEADOW, R. H.; UERPMANN, H.-P.: **Equids in the ancient world.** Beihefte zum Tübinger Atlas des Vorderen Orients. Reihe A (Naturwissenschaften) Nr. 19/2. Wiesbaden: Dr. Ludwig Reichert Verlag 1991. 333 S., zahlreiche Tab., Ktn., Taf. u. graph. Darst. 168,– DM. ISBN 3-88 226-457-8

Dem 1986 erschienenen ersten Band über die Equiden der alten Welt folgt nun der seinerzeit angekündigte zweite Band, der gleiche Zielsetzung hat: Klärung der vor- und frühgeschichtlichen Verbreitung von Pferden, Eseln und Halbeseln einschließlich ihrer domestizierten Formen in Kleinasien, im vorderen und mittleren Orient, in Nordafrika und Europa. Grundlage sind die bei Ausgrabungen geborgenen Knochen, Knochenfragmente und Zähne, deren taxonomische Zuweisung mitunter erhebliche Schwierigkeiten bereitet. Die Beiträge befassen sich mit dem Vorkommen des Afrikanischen Wildesels (*E. africanus*) in Arabien (UERPMANN), mit Equidenresten aus der südlichen Türkei und Nordsyrien (BUITENHUIS), mit Funden aus dem westlichen Iran (GILBERT) und dem frühen Auftreten von Hauspferden in Anatolien (BÖKÖNYI), mit frühholozänen Equiden aus dem Iran und der Türkei (PAYNE), mit dem ausgestorbenen *E. hydruntinus* (BONIFAY), mit dem frühesten Vorkommen von Hauseseln in Italien (BÖKÖNYI) und mit Pferdeknochenfunden in den Niederlanden (CLASON) und England (CLUTTON-BROCK, BURLEIGH). Die Knochenfunde vom bekannten Fundplatz Dereivka in der südlichen Ukraine sind erneut Gegenstand einer Erörterung über die Pferdedomestikation (ANTHONY) und schließlich wird der Versuch unternommen, mit Hilfe metrischer Verfahren an der 1. Phalanx zwischen primitiven Equiden, Zebras, Eseln, Halbeseln und Wild- und Hauspferd zu unterscheiden (DICE, EISENMANN). Die mit zahlreichen Abbildungen, Graphiken, Tabellen und umfangreichen Literaturverzeichnissen versehenen Beiträge spiegeln die ganze Bandbreite der Problematik, die einer Beschäftigung mit vorgeschichtlichen Equiden anhaftet. Trotz mancher noch offenen Fragen, die aus einer oft nicht befriedigenden Quellenlage resultieren, treten doch manche das frühere Vorkommen der verschiedenen Equiden-Arten betreffende Konturen inzwischen deutlicher hervor. Der besondere Reiz einer Beschäftigung mit dieser Thematik besteht in der engen Verzahnung von zoologisch-naturgeschichtlichen mit historisch-kulturgeschichtlichen Fakten, ohne die eine Lösung des Domestikationsproblems nicht zu erreichen ist. H. REICHSTEIN, Kiel

Deutsche Gesellschaft für Säugetierkunde: Referate, Vorträge und Posterdemonstrationen der 66. Hauptversammlung 1992

Erscheinungsweise und Bezugspreis 1993: 6 Hefte bilden einen Band. Jahresabonnement Inland: DM 378,– zuzüglich DM 13,80 Versandkosten; Jahresabonnement Österreich: öS 2940,– zuzüglich öS 140,– Versandkosten; Jahresabonnement Schweiz: sfr 364,– zuzüglich sfr 17,50 Versandkosten; Jahresabonnement EG-Binnenmarkt-Länder mit USt-ID-Nr.: DM 354,– zuzüglich DM 16,82 Versandkosten; Jahresabonnement EG-Binnenmarkt-Länder ohne USt-ID-Nr. und Drittländer: DM 378,– zuzüglich DM 18,– Versandkosten. Das Abonnement wird zum Jahresanfang berechnet und zur Zahlung fällig. Es verlängert sich stillschweigend, wenn nicht spätestens am 15. November eine Abbestellung im Verlag vorliegt. Die Zeitschrift kann bei jeder Buchhandlung oder bei der Verlagsbuchhandlung Paul Parey, Spitalerstraße 12, W-2000 Hamburg 1, Bundesrepublik Deutschland, bestellt werden. Die Mitglieder der „Deutschen Gesellschaft für Säugetierkunde“ erhalten die Zeitschrift unberechnet im Rahmen des Mitgliedsbeitrages.

Z. Säugetierkunde 58 (1993) 2, 65–128



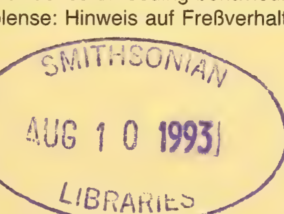
PAUL
PAREY

Vol. 58 (3), 129–200, Juni 1993 ISSN 0044-3468 C 21274 F

ZEITSCHRIFT FÜR SÄUGETIERKUNDE

INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Organ der Deutschen Gesellschaft für Säugetierkunde





Verlag Paul Parey Hamburg und Berlin

This journal is covered by Biosciences Information Service of Biological Abstracts, and by Current Contents (Series Agriculture, Biology, and Environmental Sciences) of Institute for Scientific Information

---

Die Zeitschrift für Säugetierkunde veröffentlicht Originalarbeiten und wissenschaftliche Kurzmitteilungen aus dem Gesamtgebiet der Säugetierkunde, Besprechungen der wichtigsten internationalen Literatur sowie die Bekanntmachungen der Deutschen Gesellschaft für Säugetierkunde. Verantwortlicher Schriftleiter im Sinne des Hamburgischen Pressegesetzes ist Prof. Dr. Dieter Kruska.

Zusätzlich erscheint einmal im Jahr ein Heft mit den Abstracts der Vorträge, die auf der jeweiligen Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde gehalten werden. Sie werden als Supplement dem betreffenden Jahrgang der Zeitschrift zugeordnet. Verantwortlich für ihren Inhalt sind ausschließlich die Autoren der Abstracts.

Manuskripte: Manuskriptsendungen sind zu richten an die Schriftleitung, z. Hd. Prof. Dr. Dieter Kruska, Institut für Haustierkunde, Biologiezentrum der Christian-Albrechts-Universität, Am Botanischen Garten 9, D-24118 Kiel, Bundesrepublik Deutschland. Für die Publikation vorgesehene Manuskripte sollen gemäß den „Redaktionellen Richtlinien" abgefaßt werden. In ihnen finden sich weitere Hinweise zur Annahme von Manuskripten, Bedingungen für die Veröffentlichung und die Drucklegung, ferner Richtlinien für die Abfassung eines Abstracts und eine Korrekturzeichentabelle. Die Richtlinien sind auf Anfrage bei der Schriftleitung und dem Verlag erhältlich.

Sonderdrucke: Anstelle einer Unkostenvergütung erhalten die Verfasser von Originalbeiträgen und Wissenschaftlichen Kurzmitteilungen 50 unberechnete Sonderdrucke. Mehrbedarf steht gegen Berechnung zur Verfügung, jedoch muß die Bestellung spätestens mit der Rücksendung der Korrekturfahnen erfolgen.

Fortsetzung 3. Umschlagseite

Z. Säugetierkunde 58 (1993) 129–136

ISSN 0044-3468

Diet of the Raccoon dog, *Nyctereutes procyonoides*, in Finland

By Kaarina Kauhala, Marja Kaunisto, and E. Helle

Finnish Game and Fisheries Research Institute, Helsinki and Department of Zoology, University of Oulu, Oulu, Finland

Receipt of Ms. 25.9. 1992
Acceptance of Ms. 28.10. 1992

Abstract

Studied the diet of the raccoon dog (*Nyctereutes procyonoides*) in Finland by examining the contents of 172 stomachs mainly from August–April and 206 scats from May and June. Findings suggest that the raccoon dog is a true omnivore, with the seasonal composition and diversity of the diet varying with the availability of different food items. Small mammals, plants, and carcasses and other waste were frequently eaten during all seasons, and some birds were eaten throughout the year. Insects were a common food in summer and autumn, and frogs and lizards in late spring and early summer. The diet also included fishes, particularly in early spring and autumn. The annual variation in food composition seemed to be affected by the availability of small rodents. The raccoon dog seems to be rather harmless to full-grown tetraonids and waterfowl, but the role of the raccoon dog in the predation of eggs and downy youngs of gallinaceous birds and waterfowl remains obscure.

Introduction

The raccoon dog (*Nyctereutes procyonoides* Gray, 1834) originates in the Far East, but the species was introduced to several areas in the northwest of the former Soviet Union in 1935–53 (Lavrov 1971; Helle and Kauhala 1987, 1991). From these origins the population soon spread to neighbouring countries, including Finland, and by the mid-1970s the species had colonized southern and central parts of this country. The Finnish population reached a peak in the mid-1980s. It declined slightly thereafter, but is still rather dense in southern Finland (Helle and Kauhala 1991).

The food composition of the raccoon dog has previously been studied e.g. in Japan (Ikeda 1985), in different parts of the former Soviet Union (see e.g., Bannikov 1964; Naaber 1971; Nasimovic and Isakov 1985), in the Danube Delta (Barbu 1972), in Poland (Reig and Jedrzejewski 1988) and in Finland (Viro and Mikkola 1981). The purpose of our work was to examine the annual and seasonal variation in the diet of the raccoon dog in Finland in more detail, with special reference to food composition in late spring and early summer. The diet during that period, i.e. the nesting season of birds, has been a highly controversial, but insufficiently known subject.

Material and methods

We examined 172 stomachs with some content, mainly from animals of southern and central Finland in 1986–90. Most (94 %) of the raccoon dogs were captured by hounds or earth dogs during the hunting season, which lasts from the beginning of August to the end of April. Some were found dead and some were captured in live traps. We also collected 206 scats of raccoon dogs, from the provinces of Häme and Kymi, southern Finland, in May and June 1991. The scats were taken from latrines within a radius of 150 m from the known dens of raccoon dogs.

The contents of stomachs and scats were examined after washing them with water in a sieve (0.5 mm). The food items were identified by comparing them with a reference collection and descriptions in the literature (for identifying mammals, see Day 1966; Siivonen 1974; Debrot 1982).

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5803-0129 $ 02.50/0

The frequencies of occurrence (%) of different food items in the stomachs (Tab. 1) and scats (Tab. 2) were calculated and the volume of the food items was measured. Grasses and herbs, when occurring in very small amounts, were excluded, because they had most probably been eaten accidentally. The remains of raccoon dogs, cervids, pigs or other larger mammals were defined as carcasses, as were pieces of meat with blowfly maggots, and domestic fowl (*Gallus domesticus*). With smaller animals, it is almost impossible to determine whether they had been killed by the raccoon dog itself, which means that some scavenged animals were probably included in groups for birds, mammals or fish instead of carcasses. The occurrence of carcasses of small animals and soft-structured edible waste is almost impossible to determine from scats, and thus they are probably very much underestimated in scats. The stomach data were divided into four seasons: spring (March–May, n = 53), summer (June–August, n = 10), autumn (September–November, n = 60) and winter (December–February, n = 49).

We tested seasonal and annual differences in the diet using the G test (Sokal and Rohlf 1981). We calculated Shannon-Weaver diversity indices and tested the difference between them according to Zar (1984). The frequency of occurrence of small rodents and of berries in the stomachs was compared with the availability of these food items using regression analysis. The level of significance in the tests was 0.05. The abundance indices of small rodents and wild berries were obtained from game inquiries based on abundance estimates supplied by several hundred observers throughout the country (see Helle and Kauhala 1991).

Results

Diet and its seasonal variation: stomachs

The diversity of the diet (using the seven main food categories in Tab. 1) varied somewhat with the season, being higher in the snow-free season than in winter ($P < 0.01$, diversity index for both spring and autumn was 0.78, for summer 0.77 and for winter 0.71; H'max =

Table 1. **The frequency of occurrence (%) of main food items in raccoon dog stomachs in different seasons in Finland**

Food item	Spring n = 53	Summer n = 10	Autumn n = 60	Winter n = 49	Total n = 172
Mammals	59	50	62	49	56
Rodents	43	20	43	35	40
Microtus spp.	36	20	40	20	32
Clethrionomys spp.	13	10	17	8	13
Ondatra zibethicus	6	0	2	6	4
Shrews	28	30	28	18	26
Hares	19	0	2	6	8
Birds	42	30	30	33	34
Gallinaceous birds	19	0	3	10	10
Waterfowl	0	0	3	4	2
Passerines	8	20	18	12	13
Reptiles and amphibians	6	30	12	0	8
Frogs	4	30	12	0	7
Lizards	4	20	0	0	2
Fishes	34	10	23	4	20
Invertebrates	32	80	73	37	51
Beetles	9	80	53	8	29
Wasps	4	20	17	25	15
Plants	87	100	92	86	89
Cereals	26	30	43	55	41
Berries	11	30	38	10	22
Fruits and vegetables	34	0	43	20	31
Grass and herbs	62	70	62	39	56
Carcasses and waste	47	50	48	51	49

0.85). The stomach contents were largest in autumn and smallest in winter (mean 139 ml and 53 ml, respectively).

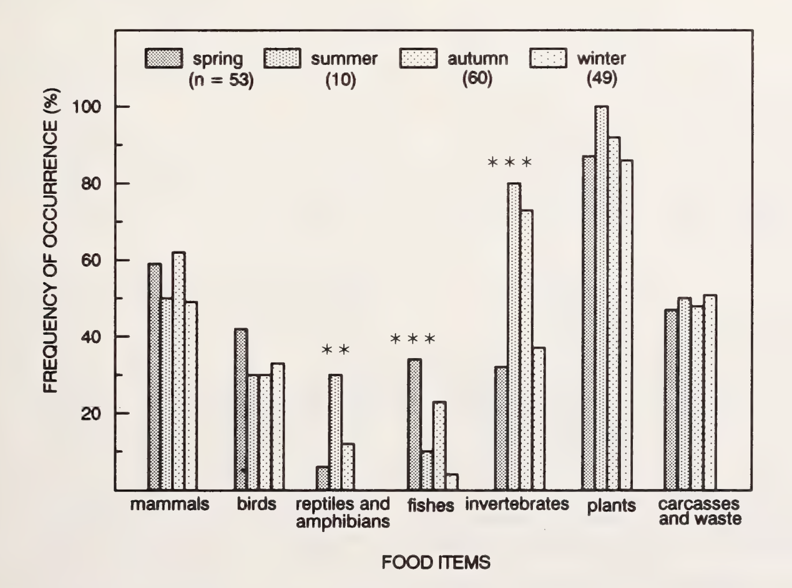
The most common food items in the stomachs were plants, invertebrates, small mammals, and carcasses and other edible waste (Tab. 1, Fig. 1). Some birds, amphibians, reptiles and fish had also been consumed, as had some inedible items. There were no statistical differences in the diet between the sexes or age groups. The only difference between the areas was noticed in the occurrence of carcasses and other waste in the stomachs: in winter and spring, these occurred more frequently in southwestern Finland than farther north ($P < 0.05$).

For seasonal comparison, we combined the data for all years because of the insignificant differences between years. The diet in summer was similar to that in autumn (however, note the small sample for summer). The food composition differed somewhat between spring, summer-autumn and winter (Tab. 1, and Fig.).

Most of the mammals consumed were small rodents, the majority being field voles (*Microtus agrestis*) and bank voles (*Clethrionomys glareolus*). There were, however, also a few muskrats (*Ondatra zibethicus*) and water voles (*Arvicola terrestris*), especially in winter, and harvest mice (*Micromys minutus*) and rats (*Rattus norvegicus*). Shrews (*Sorex* spp.) were also frequently consumed. Some hares (*Lepus* spp.) had been eaten in spring, but hardly at all in the other seasons.

Most of the birds eaten were passerines. Pheasants (*Phasianus colchicus*) were the most common gallinaceous birds, but a few black grouse (*Tetrao tetrix*) and hazel grouse (*Bonasa bonasia*) also occurred. The waterfowl identified in the stomachs were two mallards (*Anas platyrhynchos*), one teal (*Anas crecca*) and one great merganser (*Mergus merganser*).

Egg shells were found in 6 % of the stomachs, in both spring and autumn, but only once in May, when most ground nesting birds start to nest. The other egg shells most probably originated from rubbish heaps, because we found both edible and inedible waste



The frequency of occurrence of seven main food categories in raccoon dog stomachs in different seasons in Finland. The differences between seasons were tested with the G test; the statistical differences are indicated by asterisks (** means $P < 0.01$, *** $P < 0.001$)

in the same stomachs. Thus, these egg shells were most likely those of the domestic fowl, and were counted as the edible waste (Tab. 1).

Frogs (*Bufo bufo* and *Rana* spp.) and viviparous lizards (*Lacerta vivipara*) were occasionally consumed during the snow-free season. Fish occurred in the diet mainly in early spring and autumn.

Most of the invertebrates in the stomachs were insects, mainly beetles and hymenopterans. Wasps (Vespidae) were particularly abundant in winter, and beetles, e.g. Carabidae, Scarabaeidae, Silphidae and Staphylinidae, in summer and autumn. Some ants, earthworms and mollusks had also been consumed.

In spring and early summer, the plant material consumed was mostly grass and other vegetative parts of plants, but in late summer and autumn it was mainly cereal grains, berries, vegetables and fruits. The berries were mostly blueberries (*Vaccinium myrtillus*), lingonberries (*V. vitis-idaea*) and cultivated berries (frequency of occurrence of berries was 52 % in August-October). In winter most of the plant material consumed was cereal grains.

Carcasses and other edible waste (apart from the eggs) were domestic fowl and mammals, e.g. other canids (the red fox and the raccoon dog) and cervids.

Diet in the nesting season of birds: scats

In May and June the most frequent food items in the scats were small mammals (Tab. 2). The majority were voles, but shrews also frequently occurred. Some remains of hares were found. No gallinaceous birds were identified in the scats and we found remains of adult waterfowl in two scats only. Ninety-four percent of the birds were identified as passerines; one bird could not be identified. Some scats contained very small pieces of egg shells, from an unidentified species.

Frogs and viviparous lizards were common in the scats. Almost all the invertebrates found were either beetles or wasps. Most of the plants identified were herbs and grass. Animals classified as carcasses occurred only rarely (4 %) in the scats in May and June. Separate hairs of raccoon dogs were found in 54 % of the scats and in very small amounts; these hairs were probably swallowed, when the raccoon dogs were cleaning their furs.

Table 2. **The frequency of occurrence (%) of main food items in raccoon dog scats (n = 206) collected in southern Finland in May and June 1991**

Food item	Frequency of occurrence
Mammals	76
Rodents	52
Shrews	30
Hares	6
Birds	23
Passerines	23
Waterfowl	1
Eggs	9
Reptiles and amphibians	53
Frogs	43
Lizards	39
Fishes	18
Invertebrates	72
Beetles	66
Wasps	18
Plants	22
Cereals	8
Berries	3
Grass and herbs	13

Annual variation in the diet

Apart from some minor changes, the food composition remained rather similar from year to year. The frequency of occurrence of small rodents in the stomachs correlated positively with their abundance index in autumn in southern Finland ($r = 0.96$, $P < 0.05$), being highest in 1988 and lowest in 1987. In contrast to small mammals, the frequency of occurrence of hares in the diet was higher in spring 1987 than in spring 1988 ($P < 0.001$). Although the frequency of occurrence of berries seemed to correlate

with their abundance index in southern Finland (r = 0.77), the correlation was not significant, which, however, may be due to the small sample size.

Discussion

Omnivory of the raccoon dog

The raccoon dog is a true omnivore; the availability of different food items affects both seasonal and annual composition and diversity of the diet. Thus, the raccoon dog probably does not have strong preferences for any food items, except possibly small mammals and berries.

Our results confirm those of other studies: the raccoon dog is omnivorous and the food composition varies somewhat with the area, season and year. However, small mammals, invertebrates and plants seem to be among the commonly consumed food items in most areas (Bannikov 1964; Nasimovic and Isakov 1985), except in Japan, where fish and other marine animals, algae, insects and, during certain seasons, fruits are the main food sources (Ikeda 1985). Frogs are also important prey in some areas (Korneev 1954; Barbu 1972; Viro and Mikkola 1981). Birds are eaten to some extent in most areas, but they are not among the most frequent food items in any larger area. The role of carcasses in the diet seems to be rather insignificant in all areas except Finland, scavenging having only occasionally been reported elsewhere (Sviridov 1958; Kostoglod 1972), but this may be due to the method used. However, cannibalism is known to occur in other areas also (Nasimovic and Isakov 1985).

It can be deduced from the morphology that the raccoon dog is a gatherer rather than a predator. Some characteristics of carnivores are only poorly developed (Bannikov 1964). The intestine is 1.5–2 times longer than of other canids, the canines are small, the carnassial blades are short, and the molars are large. The raccoon dog is also rather short-legged and clumsy.

Seasonal and annual variation in the diet

The significance of small mammals was probably greatest in spring and autumn; in summer the food supply is so abundant that small mammals are not essential for the raccoon dog. In years when small rodents are scarce, they are to some extent replaced. e.g., by hares. Outside Finland, too, the annual variation in the diet seems to be mostly dependent on the availability of small rodents (Morozov 1947; Popov 1956; Geller 1959; Ivanova 1962).

The importance of small mammals as food is seen in the fact that the availability of small rodents even seems to explain some of the annual variation in the numbers of raccoon dogs in Finland (Helle and kauhala 1991). The abundance of voles affects the fat reserves of females in spring (Kauhala, unpubl.) and, thus, the productivity of the population. The abundance of small rodents may also have an effect on the growth and mortality of juveniles.

Birds seem to be of some importance for the raccoon dog in all seasons. However, it is very difficult to establish to what extent the raccoon dogs feed on eggs, because they may break large eggs, and only lap up their contents. The authors have noticed such behaviour among farmed raccoon dogs.

Frogs and lizards are an important food source for the raccoon dog in late spring and early summer, but rather unimportant in other seasons. It is not easy to find remnants of tadpoles or frogspawn in stomachs or scats, and thus the study may underestimate the significance of frogs.

The occurrence of fish in the diet in early spring may be explained by the fact that fish are readily available for the raccoon dogs at that time; ice-fishing is popular in Finland and small fish are often left by fishermen beside the hole on the ice. Tracks of raccoon dogs are

commonly seen on the ice in early spring, when raccoon dogs feed on these fish. These fish may constitute a valuable addition to the diet in some areas, as they are available at a time when other food sources are scarce, and the energy requirement, particularly that of pregnant females, is high.

Invertebrates were frequently eaten in the snow-free season as observed earlier in Finland (Viro and Mikkola 1981). Our study may overestimate the frequency of invertebrates, some of them possibly having been in the stomachs of frogs and lizards eaten by the raccoon dog. On the other hand, a major part of insects eaten consisted of large beetles (Carabidae and Scarabaeidae) that most probably had been caught by the raccoon dogs themselves. Furthermore, the small size of invertebrates compounds the difficulty of assessing their importance as a food source for the raccoon dog, as the frequency of occurrence may be misleading. For instance, the occurrence of invertebrates during summer and autumn was 74 %, whereas their proportion by volume was only 6 %. But volume, also, can be misleading, as it is greatly affected by the time elapsing since the last meal and the digestibility of food (Englund 1965).

Plants are an important year-round food source for the raccoon dog. Of particular interest is the role of berries in the diet of the raccoon dog; half of the stomachs in August-October contained them. This figure probably underestimates the real importance of berries, because berries are easily digested and do not remain for long periods in the stomachs. Berries seemed to be most common in the stomachs in 1988, a year of abundant blueberries and lingonberries. Nasimovic and Isakov (1985) point out that the crop of berries and fruits can affect the yearly variation in the diet. And further, the abundance of berries seems to affect even the yearly variation in numbers of raccoon dogs, as it most probably affects the mortality of juveniles during their first autumn and winter and, thus, the population density in the following spring (Helle and Kauhala 1991).

Almost half of the stomachs contained carcasses or other edible waste, indicating the importance of carcasses and rubbish heaps to the raccoon dog. The occurrence of various inedible items, including rubber bands, and pieces of newspaper and plastic, in the stomachs also indicates frequent visits to rubbish heaps. Rubbish heaps seem to be important in all seasons, but most of all in winter and early spring, when there is a shortage of other food. According to Viro and Mikkola (1981), carcasses were the most important food source for raccoon dog in winter, but not during the snow-free season. In our study, waste and carcasses were more commonly consumed in southwestern Finland than farther north. This is a result of higher availability of such sites due to dense human population. Winters are also warmer in the south, and raccoon dogs sleep for a shorter period. As a result, they are actively moving around in winter and early spring, when other food sources are scarce.

Small game animals in the diet

This study provides no evidence that the raccoon dog is highly harmful to game bird populations. The birds most commonly identified in the stomachs and scats were passerines; there were no remains of tetraonids in scats in May and June. However, we did find some gallinaceous birds in the stomachs in spring. Moreover, there were some remains of waterfowl in the scats, so the raccoon dog may have killed incubating females. (The raccoon dog is most likely unable to catch other healthy adult birds.) It is of course possible that the birds had been found dead. However, as mentioned above, we do not have much knowledge of egg predation by the raccoon dog in Finland.

We found remains of waterfowl in the stomachs only in autumn and winter. They had most probably been injured or were dead because we sometimes found shots in the same stomachs, as did Naaber (1974) in Estonia.

Obtemperanskij (1958) found birds only in 3 % of the scats in a forest area in Voronez (European Russia) in late spring and early summer. However, Ivanova (1962) found

remains of birds in 45 % of the scats in a river valley in the same large area. Most of these birds were waterfowl, but a few passerines and domestic fowl were also found. Pieces of egg shells were rarely found (in 3 % of the scats).

NAABER (1971, 1984) found that in some sites in Estonia raccoon dog can be very harmful to waterfowl; they have robbed even 85 % of the nests. In the Matsalu area (seashore nature reserve area) birds occurred in 31 % and egg shells in 33 % of the scats in spring. However, according to NAABER (1971) the raccoon dog appeared to be harmless to other game animals, such as gallinaceous birds and hares.

REIG and JEDRZEJEWSKI (1988) compared the diets of five mammalian predators in Bialowieza National Park in Poland in winter and spring. They found that more than 90 % of the birds preyed upon were eaten by the red fox. Also NAABER (1974) considered the red fox much more harmful to game animals than the raccoon dog. In the Far East, JUDIN (1977) found birds in 5–20 % of the scats in spring, 4–6 % in summer, the proportion of gallinaceous birds and waterfowl ranging from 0–4 %. These findings from other localities also support the idea that the raccoon dog poses little danger to game birds in most areas, but it may be harmful in some special sites, e.g., in waterfowl colonies.

The few hares in the stomachs and scats were probably juveniles, because hares occurred in the stomachs mostly in spring, and adult hares are far too quick to be caught by the raccoon dog. We found remains of hares only in four stomachs in autumn and winter, and it is questionable whether the raccoon dogs themselves had killed these hares or if the hares had been killed, e.g., by traffic.

Acknowledgements

We thank all those hunters who sent us raccoon dog carcasses, and S. PUONTI who collected scats for us. We are also grateful to H. and R. KOIVUNEN for technical assistance, to K. HUHTALA for helping us to identify the remains of birds and some mammals, to J. MUONA for identifying the beetles, and to J. SIEKKINEN for identifying the other food items in the scats. We are much obliged to P. VIRO and S. SULKAVA for the valuable advice they gave us in the course of our work. We are grateful to the Academy of Finland (Research Council for Agriculture and Forestry), the Nordic Council for Wildlife Research and the Finnish Game Foundation for financial support.

Zusammenfassung

Die Nahrung des Marderhundes, Nyctereutes procyonoides, in Finnland

Die Nahrung des Marderhundes (*Nyctereutes procyonoides*) in Finnland wurde untersucht, indem hauptsächlich von August bis April der Inhalt von 172 Mägen und im Mai und Juni 206 Kotballen analysiert wurden. Die Befunde weisen darauf hin, daß der Marderhund ein typischer Allesfresser ist, bei dem die saisonale Zusammensetzung und Vielfalt der Nahrung je nach Verfügbarkeit der verschiedenen Nahrungsbestandteile variiert. Kleine Säugetiere, Pflanzen, Aas und andere Abfälle fraß der Marderhund zu allen Jahreszeiten häufig, und auch einige Vogelarten dienten ihm rund um das Jahr als Nahrung. Insekten waren im Sommer und im Herbst eine häufige Nahrung Frösche und Eidechsen im späten Frühling und im Frühsommer. Zur Nahrung gehörten auch Fische, vor allem im Frühling und Herbst. Die jährliche Variation in der Zusammensetzung der Nahrung schien vom Vorhandensein kleiner Nagetiere abzuhängen. Für erwachsene Tetraoniden und Wasservögel scheint der Marderhund weitgehend ungefährlich zu sein, aber inwieweit er für den Raub von Eiern und Brut der Hühner- und Wasservögel verantwortlich ist, bleibt nach wie vor unklar.

References

BANNIKOV, A. G. (1964): Biologie du chien viverrin en U.S.S.R. Mammalia **28**, 1–39.

BARBU, P. (1972): Beiträge zum Studium des Marderhundes, *Nyctereutes procyonoides ussuriensis* Matschie, 1907, aus dem Donaudelta. Säugetierkdl. Mitt. **20**, 375–405.

DAY, M. G. (1966): Identification of hair and feather remains in the gut and faeces of stoats and weasels. J. Zool. (London) **148**, 201–217.

DEBROT, S. (1982): Atlas des poils de mammiferès d'Europe. Neuchâtel: Institut de Zoologie de l'Université de Neuchâtel.

Englund, J. (1965): Studies on food ecology of the red fox (*Vulpes vulpes*) in Sweden. Viltrevy **3**, 377–485.
Geller, M. H. (1959): Biologija ussurijskogo enota (*Nyctereutes procyonoides* Gray), akklimatizirovannogo na Severo-Zapade Evropejskoj casti SSSR. Tr. NII sel. hoz-va Krajnego Severa 9.
Helle, E.; Kauhala, K. (1987): Supikoiran leviämishistoria ja kantojen nykytila Suomessa. Suomen Riista **34**, 7–21.
— (1991): Distribution history and present status of the raccoon dog in Finland. Holarctic Ecology **14**, 278–286.
Ikeda, H. (1985): Regime alimentaire et domaine vital du chien viverrin au Japon. Rev. Ecol. **40**, 165–169.
Ivanova, G. I. (1962): Sravnitel'naja harakteristika pitanija lisicy, barsuka i enotovidnoj sobaki v Voronezskom zapovednike. Uch. Zap. Mosk. Gos. Pedagog. Inst. Lenina **186**, 210–256.
Judin, V. G. (1977): Enotovidnaja sobaka Primor'ja v Priamur'ja. Moscow: Nauka.
Korneev, A. I. (1954): Enotovidnaja sobaka *Nyctereutes procyonoides* Gray na Ukraine (rezul'taty rabot po akklimatizacii). Tr. Zool. muzeja Kiev. un-ta im. T. G. Sevcenko 4.
Kostlogov, V. E. (1972): Enotovidnaja sobaka v priazovskih plavnjah Kubani. Tr. VNII ohotnic'ego hoz-va i zverovodstva 24.
Lavrov, N. P. (1971): I togi introduktsii enotovidnoj sobaki (Npg) v otdel'nye obblasti SSSR. Trudy kafedry biologii MGZPI **29**, 101–160.
Morozov, V. F. (1947): Akklimatizacija ussurijskogo enota (*Nyctereutes procyonoides* Gray) v Leningradskoj i Novgorodskoj oblastjah. Tr. VNII ohotnic'ego promysla **8**, 111–124.
Naaber, J. (1971): Kährikkoer. Eesti Loodus **14**, 449–455.
— (1974): Rebane ja kährikkoer meie looduses. In: Jaht ja Ulukid. Eesti NSV jahimeeste seltsi aastaraamat 1969–1972. Ed. by G. Merisalu. Tallinn: Eesti NSV Jahimeeste Selts.
— (1984): Matsalu imetajatefauna olevikust ja tulevikust. In: Eesti NSV Riiklike Looduskaitsealade Teaduslikud Tööd IV, Matsalu loodusest. Ed. by V. Paakspuu. Tallinn: Valgus.
Nasimovic, A. A.; Isakov, J. A. (eds.) (1985): Pesec, lisica, enotovidnaja sobaka: Razmescenie zapazov, ekologija, ispol'zovanie i ohrana. Moscow: Nauka.
Obtemperanskij, S. I. (1958): O nekotoryh osobennostjah razmnozenija enotovidnoj sobaki v uslovijah Voronezskoj oblasti. Tr. Voronez. un-ta 56.
Popov, Ju. K. (1956): Materialy po ekologii enotovidnoj sobaki (*Nyctereutes procyonoides* Gray) v Tatarskoj ASSR. Ivz. Kazan. fil. AN. SSSR. Ser. biol. nauk 5.
Reig, S.; Jedrzejewski, W. (1988): Winter and Early Spring Food of Some Carnivores in the Bialowieza National Park, Eastern Poland. Acta Theriol. **33**, 57–65.
Siivonen, L. (1974): Pohjolan nisäkkäät. Keuruu: Otava.
Sokal, R. R.; Rohlf, F. J. (1981): Biometry: the principles and practice of statistics in biological research. San Francisco: W. H. Freeman.
Sviridov, I. S. (1958): Pitanie enotovidnoj sobaki, akklimatizirovannoj v Niznem Povoloz'e i na Severnom Kavkaze. Izv. Irkut. s.-h. in-ta 8.
Viro, P.; Mikkola, H. (1981): Food composition of the raccoon dog *Nyctereutes procyonoides* Gray, 1834 in Finland. Z. Säugetierkunde **46**, 20–26.
Zar, J. H. (1984): Biostatistical analysis. Englewood Cliffs, New Jersey: Prentice-Hall.

Authors' addresses: Kaarina Kauhala and Eero Helle, Finnish Game and Fisheries Research Institute, Game Division, P.O. Box 202, SF-00151 Helsinki, Finland; Marja Kaunisto, Department of Zoology, University of Oulu, Linnanmaa, SF-90570 Oulu, Finland

Z. Säugetierkunde 58 (1993) 137–143

ISSN 0044-3468

Pine marten (*Martes martes* L.) home ranges and activity patterns on the island of Minorca, Spain

By A. P. Clevenger

Department of Forestry, Wildlife and Fisheries, The University of Tennessee, Knoxville, USA

Receipt of Ms. 23. 4. 1992
Acceptance of Ms. 22. 6. 1992

Abstract

The home range and activity patterns of European pine marten (*Martes martes* L.) on the island of Minorca (Spain) were studied between October 1990 and March 1991. Female home ranges (n = 3) were non-overlapping and averaged 47.3 ha (range = 31.5–66 ha); two male home ranges were partially exclusive, measuring 492 ha and 919 ha. Male home ranges averaged 16 times greater than females. Pine marten were primarily nocturnal, being active 53 % and 59 % of the nighttime hours during Autumn/Winter and Spring, respectively; daytime activity levels were 19 % and 14 % during each season, respectively. Diel activity for all martens averaged 34 %. Although the data are limited, they have shown that the Minorcan pine marten may have a relationship between home range size, activity, and site conditions which merits further study.

Introduction

Members of the genus *Martes* are generally considered intrasexually territorial with overlapping home ranges between sexes (Hawley and Newby 1957; Powell 1979; Buskirk and MacDonald 1989). The degree of territoriality may be affected by such factors as food availability, habitat, and sexual activity and can break down under certain conditions (Lockie 1966). It has been suggested that *Martes* spacing patterns may be flexible, and the degree of territoriality varies with prey population density (Powell 1991).

The size of foods and their availability have been shown to affect North American pine martens (*M. americana*) daily activity patterns (Strickland et al. 1982). For the same species, Zielinski et al. (1983) found that activity was synchronized with the activity of their prey. At present, few studies of the European pine martens (*M. martes*) home range have been conducted (Storch 1988; Marchesi 1989; Kruger 1990; Balharry 1991) and data on activity patterns are even more limited (Marchesi 1989). In this study, I present home range and activity pattern data from an insular, terrestrial competitor-free population of pine marten in the southern extreme of the species range.

Material and methods

The island of Minorca is part of the Balearic Island group located in the western Mediterranean approximately 250 km from the Iberian Peninsula. It measures 69 000 ha and is approximately 45 km long and 15 km wide. The study took place in a 29 km^2 area along the islands north coast. The climate is humid mediterranean with moderate temperatures. The island vegetation is also mediterranean, consisting of Aleppo pine (*Pinus helepensis*) and holm oak (*Quercus ilex*) forests, coastal shrublands and pastureland. Typical shrub species include wild olive (*Olea europaea*), lentisc (*Pistacia lentiscus*) and tree heather (*Erica arborea*). Much of the island consists of subdivided grazing pastures used by dairy cows.

Fieldwork was conducted from October 1990 to March 1991. A total of five pine martens were captured in padded Victor 1½ "Soft-catch" leg-hold traps (Woodstream Corporation, Lititz, Penn-

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5803-0137 $ 02.50/0

sylvania, U.S.A.) baited with partial or whole chickens. Pine martens were physically immobilized with the assistance of another person and using heavily padded gloves. Ages of captured pine martens were not determined. All captured individuals were equipped with 150–152 Mhz motion-sensored radiotransmitter collars (Type P2B, AVM Instrument Co., Livermore, California, U.S.A.; A. Urmeneta, Argüedas, Navarra, Spain) and monitored with Telonics TR-2 receivers and 2-element Yagi antennas (Telonics Inc., Mesa, Arizona, U.S.A.).

Martens were located by triangulation on the direction of the radio signal from points on the ground. The observation-area curve (Odum and Kuenzler 1955) was plotted for all pine marten home ranges to determine at what point they reached an asymptote (less than 10 % increase/10 radiolocations). Home ranges were estimated using the minimum convex polygon method (Mohr 1947) with the McPAAL PC program (M. Stüwe, Smithsonian Institution, Front Royal, Virginia, U.S.A.). Radiolocation data were divided into two seasons: Autumn/Winter = 25 October–15 February, and Spring = 16 February–1 April.

Pine marten activity was monitored by recording changes in signal modes and signal variations due to the movements of the animals (Zielinski et al. 1983). Data was obtained sporadically while carrying out other field activities and by nine continuous monitoring sessions of 6–24 hour periods during which readings were taken every 15–30 minutes. Due to data limitations, daily activity was pooled into two periods for the two seasons indicated above. Time periods were determined by calculating the average hour of sunrise and sunset for each period and were as follows, Autumn/Winter: Day = 0720–1805 h, Night = 1806–0719 h; Spring: Day = 0650–1915 h, Night = 1916–0649 h. Activity was defined as the percentage of observations that indicated movement and statistical differences were assessed using Wilcoxan signed rank tests (Sokal and Rolf 1981).

Results

During the five months of fieldwork reported here, data were collected from five pine martens (2 males, 3 females) for a total of 255 marten/days. Individual pine martens were monitored for an average of 51 days (range = 5–152, SD = 59 days); during Autumn/Winter and Spring the radiomarked martens consisted of 1 male and 2 females. One of the females (F2) was radiotracked both seasons.

The home range area asymptote was obtained by female pine marten F2 during both Autumn/Winter and Spring (Fig. 1). The home ranges of males M3 and M4 appeared to be reaching asymptote as they did not increase more than 10 % in the final eight and nine radiolocations, respectively. Female pine martens F1 and F5 did not reach maximum home range size during the study period; however, because the former was nearing asymptote it was included in the calculations. I opted to not include F5 in the calculations as only five radiolocations were obtained but her home range was plotted as its spatial relation to the other female martens was noteworthy.

A total of 92 radiolocations were used in estimating all pine marten home ranges; 49 during Autumn/Winter and 43 in Spring. The average time between successive radiolocations was 2.3 ± 0.4 (± SE) days. There was great discrepancy between male and female home ranges. The Autumn/Winter home ranges of two females measured 31.5 and 66.5 ha (n = 20 and 12 radiolocations, respectively) while the one male used 492 ha (n = 17

Average percentage of time pine martens were active during daytime, nighttime, and total periods by season in Minorca, Spain

Total number of activity readings are given in parentheses

	Day Male/Female/Total	Night Male/Female/Total	Total Male/Female/Total
Autumn/Winter	25.0/17.4/18.9 (104)(270)(374)	41.5/58.8/53.1 (53)(107)(160)	29.2/29.1/29.2 (157)(378)(534)
Spring	13.3/14.8/14.1 (127)(128)(255)	53.0/64.1/59.0 (90)(117)(207)	29.9/38.3/34.4 (217)(245)(462)

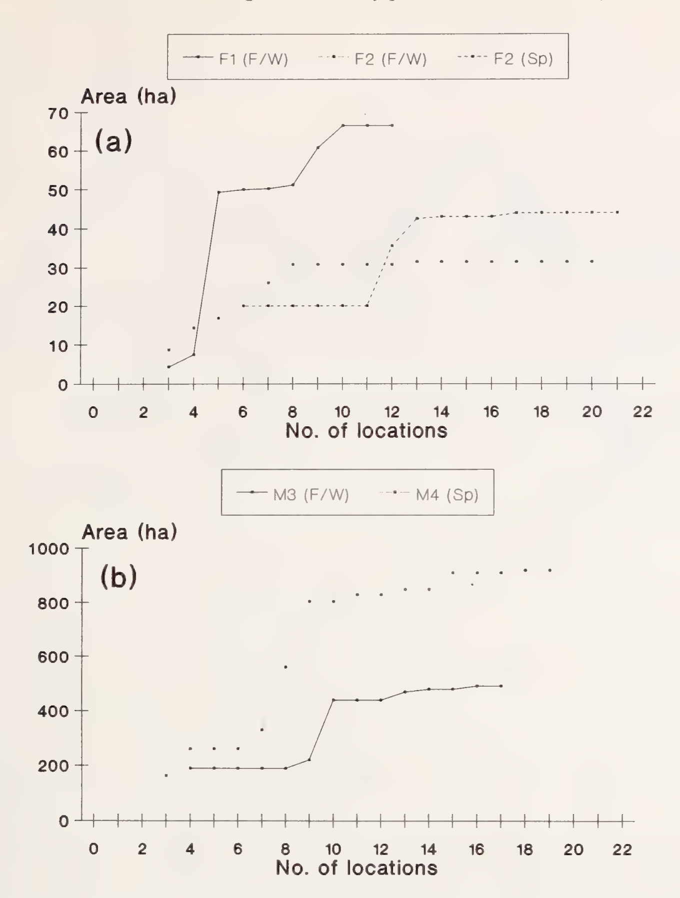


Fig. 1. Asymptote home range sizes of female (a) and male (b) pine martens radiotracked on the island of Minorca, Spain, 1990–1991

locations) (Fig. 2). Likewise during Spring, one female had a home range of 44 ha (n = 21 locations) and that of a male measured 919.5 ha (n = 19 locations). For the 5-month period, female home range estimates averaged 47.3 ha (range = 31.5–66.5 ha, n = 3) and males 705.7 ha (range = 492–919.5 ha, n = 2). Female home ranges did not overlap, and the two male ranges did so only slightly. Male home ranges averaged 16 times greater than females (range = 7–29 times) and each included the range of at least one of the radiomarked females.

A total of 996 readings were used in the analysis of activity patterns. There was no significant difference in seasonal activity patterns ($P > 0.10$) as all pine martens were primarily nocturnal during both seasons. During Autumn/Winter they were 19 % daytime active vs. 53 % nighttime, and in Spring 14 % daytime active vs. 59 % nighttime (Table). Pine martens were active 29 % of the time during Autumn/Winter; the one male was slightly more diurnal than the two females (25 % vs. 17 %). Females showed more activity during the nighttime hours (58 % vs. 41 %). During Spring, activity did not differ significantly from the previous season ($P > 0.10$). Total pine marten activity averaged 34 %, both females being more active than the male (38 % vs. 30 %). There was no difference between daytime activity levels of the pine martens; however nocturnal activity was greater for the two females than for the male (64 % vs. 53 %).

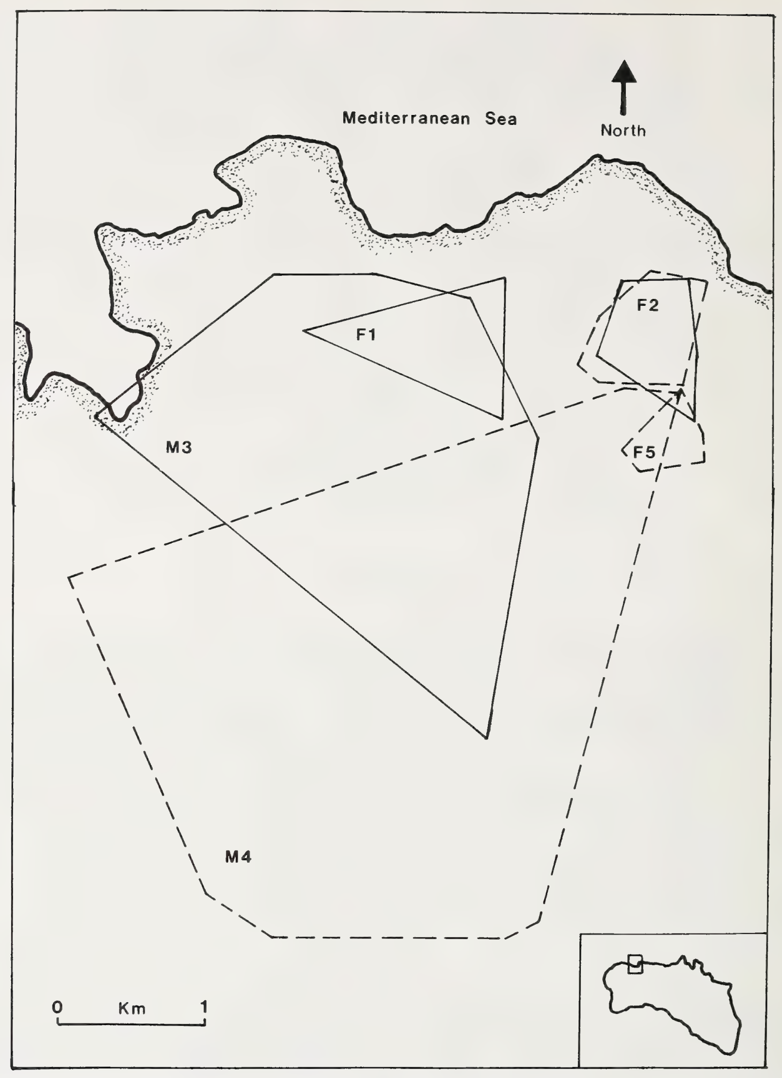


Fig. 2. Home ranges of three female (F) and two male (M) pine martens on the island of Minorca, Spain, 1990–1991. Solid line = Autumn/Winter and broken line = Spring

Discussion

The radiomonitored pine martens in Minorca appeared to be intrasexually territorial, with overlap of home ranges between sexes as reported in other European studies (Storch 1988; Marchesi 1989; Kruger 1990; Balharry 1991). The two male home ranges were shown to overlap slightly; however most of the shared area is open pastureland, and it is unlikely that it is regularly used. All but one of M3's radiolocations were located on the mountainous north side of the study area while M4 concentrated his activities on the south side of La Vall. Since both male martens were monitored during separate periods, their true spatial relationship may not be accurately shown here.

Female pine martens home ranges did not overlap and occupied a relatively small size. The home range of F5 is probably underestimated, as only five radiolocations were used in the calculation.

The male and female pine marten home range estimates in Minorca were much smaller than those reported for the species throughout the rest of Europe. However, the results presented come from a small sample size, a limited amount of data, and caution must be taken in interpreting them. In Germany, KRUGER (1990) reported two female pine martens with home ranges of 760 and 960 ha, while a male covered 1500 ha. In two different areas in Scotland, male pine marten home ranges varied from 400–600 ha (n = 5) to 2000–3000 ha (n = 6) (BALHARRY 1991). Other studies have described female ranges as being 200–1000 ha, and male ranges as 900–2000 ha (STORCH 1988; MARCHESI 1989). Because home range data from island mammal populations are scarce, more will be needed for comparing with mainland data to determine whether this may be a general phenomenon.

The use of space has been proposed as being a good indicator of habitat quality (LINDSTEDT et al. 1986; BUSKIRK and MACDONALD 1989; ZIELINSKI 1991). Highly productive and dense populations of pine martens, should be found in high quality habitats and should therefore have small home ranges. In Minorca, pine martens have no competitors for the seasonally abundant foods which constitute their diet (CLEVENGER 1992), which may explain the small home ranges reported in this study.

The most surprising result was the reduced female home ranges in comparison with male home ranges on the island. A male pine marten in Germany used an area 1.5 and 1.9 times greater than did two females respectively (KRUGER 1990). In seven North American pine marten home range studies, male home ranges averaged 2.4 times (range = 1.1–3.4 times) greater than those of females (HAWLEY and NEWBY 1957; FRANCIS and STEPHENSON 1972; CLARK and CAMPBELL 1977; WYNNE and SHERBURNE 1984; LINDSTEDT et al. 1986; BAKER 1991; LATOUR et al. 1991). In Minorca, male home range estimates were not substantially smaller than those of other *Martes* populations cited above. Because female home ranges are dependent on food abundance and distribution, these data suggest that the island prey populations may be less dispersed than in areas occupied by other marten populations, and that the Minorcan pine marten lives in a high quality habitat. Male home range size therefore does not appear to be influenced by food abundance and distribution but may likely be determined by the maximum number of females a male marten can include within its home range.

European pine martens have been described as being normally nocturnal or crepuscular (LABRID 1986), but quantitative data are lacking. For pine martens, factors such as temperature, amount of human activity, size and abundance of prey items are believed to affect activity behaviour. Unlike in other parts of its' range, temperature is not a stress factor in the Balearic Islands. Human activity is extremely low in the study area. Therefore, the types of food that marten may be consuming and the foraging strategies used to obtain them, may be important factors regulating activity in Minorca.

Principal foods in Autumn/Winter are fleshy fruits, insects and small mammals, whereas during sprisng small mammals and birds are favored (CLEVENGER 1992). It also has been suggested that, where these foods are abundant and not widely distributed, martens should have low activity levels (THOMPSON 1987; ZIELINSKI 1991; see also HUTTO 1990). If this is true, it does not entirely agree with home range habitat quality relationship mentioned earlier, since the nighttime activity levels reported herein appear to be high compared with those of *M. americana* (ZIELINSKI 1983). The high nighttime activity might be explained by the Minorcan martens focusing on nocturnal prey (small mammals), being relatively inefficient predators, or their having higher than normal energy requirements due to this race's exceptionally large size (ALCOVER et al. 1986).

Evidently more study is needed on the foraging behaviour and activity patterns of Minorcan pine marten with respect to their prey in order to help clarify some of the

hypotheses regarding pine marten utilization of space and time as an indicator of habitat quality. Given that in Minorca pine marten have no terrestrial competitors, and temperature and human activity can be discounted as significant factors increasing their metabolic demands, this island situation may serve as an opportune area in which to delve further into these questions.

Acknowledgements

Funding for this research was provided by a grant from Spain's Ministry of Education and Science (CICyT). I would like to thank Carmen Campos, Miguel Angel Campos, Alejandro Onrubia and Rafael Triay for their field assistance, Ricardo Squella for permission to conduct this study in La Vall, and Francisco J. Purroy and Michael R. Pelton for their cooperation in various aspects of the study. William J. Zielinski critically reviewed an early draft of the manuscript. Finally I am grateful to Jacques and Anne-Marie Teinturier for allowing me to use their house while in Minorca.

Zusammenfassung

Streifgebiete und Aktivitätsmuster der Baummarder (Martes martes L.) auf der Insel Minorca, Spanien

Auf der Insel Minorca, Balearen, wurden von Oktober 1990 bis März 1991 die Streifgebiete und die Aktivität von fünf mit Radiosendern markierten Baummardern (3 ♀, 2♂) untersucht. Die Streifgebiete der Weibchen waren 47.3 ha (31.5–66 ha) groß und überschnitten sich nicht; die zweier Männchen waren 492 ha und 919 ha groß und überschnitten sich zum Teil. Die Gebiete der Männchen waren im Mittel 16mal größer als die der Weibchen. Die Baummarder waren im Untersuchungszeitraum überwiegend nachtaktiv; in den Perioden Herbst/Winter und Frühjahr waren sie 53 % bzw. 59 % der Nachtstunden und 19 % bzw. 14 % der Tagstunden aktiv. Die tägliche Gesamtaktivität betrug 34 %. Die vorliegenden Beobachtungen weisen einige interessante Aspekte auf, die ein vertieftes Studium der Marder Minorcas wünschenswert erscheinen lassen.

References

Alcover, J. A.; Delibes, M.; Gosálbez, J.; Nadal, J. (1986): *Martes martes* Linnaeus, 1758 a les Balears. Misc. Zool. **10**, 323–333.

Baker, J. (1991): Spatial organization and seasonal habitat use of marten on southern Vancouver Island, British Columbia. In: Abstracts, Symposium on the Biology and Management of Martens and Fishers. Ed. by S. W. Buskirk. Laramie: University of Wyoming. Pp. 5.

Balharry, D. (1991): Group stability and intrasexual territoriality in pine martens (*Martes*). In: Abstracts, Symposium on the Biology and Management of Martens and Fishers. Ed. by S. W. Buskirk. Laramie: University of Wyoming. Pp. 8.

Buskirk, S. W.; MacDonald, L. L. (1989): Analysis of variability in home range size of the American marten. J. Wildl. Manage. **53**, 997–1004.

Clark, T. W.; Campbell, T. M. (1976): Population organization and regulatory mechanisms of martens in Grand Teton National Park, Wyoming. Nat. Park Serv. Transact. Proc. **1**, 293–295.

Clevenger, A. P. (1992): Spring and summer food habits and habitat use of the European pine marten on the island of Minorca, Spain. J. Zool. Lond. (in press).

Francis, G. R.; Stephenson, A. B. (1972): Marten ranges and food habits in Algonquin Provincial Park, Ontario. Ontario Min. of Nat. Resour. Res. Rept. **19**, 1–53.

Hawley, V. D.; Newby, F. E. (1957): Marten home ranges and population fluctuations. J. Mammalogy **38**, 174–184.

Hutto, R. L. (1990): Measuring the availability of food resources. Stud. Avian Biol. **13**, 20–28.

Kruger, H.-H. (1990): Home ranges and patterns of distribution of stone and pine martens. Trans. Int. Union of Game Biol. Congress **19**, 348–349.

Labrid, M. (1986): La martre (*Martes martes* Linnaeus, 1758). Encyclopedie des carnivores de France, No. 9.

Latour, P.; MacLean, N.; Poole, K. G. (1991): Movements of marten in burned and unburned taiga of the western Northwest Territories. In: Abstr., Symposium on the Biology and Management of Martens and Fishers. Ed. by S. W. Buskirk. Laramie: University of Wyoming. Pp. 50.

Lindstedt, S. L.; Miller, B. J.; Buskirk, S. W. (1986): Home range, time, and body size in mammals. Ecology **67**, 413–418.

Lockie, J. D. (1966): Territory in small carnivores. Symp. Zool. Soc. Lond. **18**, 143–165.

Marchesi, P. (1989): Ecology of the pine marten (*Martes martes* L.) in the Swiss Jura Mountains. D. Sc. thesis, Univ. Neuchâtel, Switzerland.

Mohr, C. O. (1947): Table of equivalent populations of North American small mammals. Am. Midl. Nat. **37**, 223–249.

Odum, E. P.; Kuenzler, E. J. (1955): Measurement of territory and home range size in birds. Auk **72**, 128–137.
Powell, R. A. (1979): Mustelid spacing patterns: variations on a theme by *Mustela*. Z. Tierpsychol. **50**, 153–165.
Powell, R. A. (1991): Structure and spacing of Martes populations. In: Abstracts, Symposium on the Biology and Management of Martens and Fishers. Ed. by S. W. Buskirk. Laramie: University of Wyoming. Pp. 64.
Sokal, R. R.; Rolf, F. J. (1981): Biometry. San Francisco: W. H. Freeman.
Storch, I. (1988): Home range utilization by pine martens. Z. Jagdwiss. **34**, 115–119.
Strickland, M. A.; Douglas, C. W.; Novak, M.; Hunziger, N. P. (1982): Marten, *Martes americana*. In: Wild mammals of North America. Ed. by J. Chapman and G. A. Feldhamer. Baltimore, Maryland: The John Hopkins University Press. Pp. 599–612.
Thompson, I. D. (1987): Effects of logging on marten hunting activity and use of home range. Trans. Int. Union of Game Biol. Congress **18**, 202–203.
Wynne, K. M.; Sherburne, R. M. (1984): Summer home range use by adult marten in Northwestern Maine. Can. J. Zool. **62**, 941–943.
Zielinski, W. J. (1991): Behavioral indicators of marten population stress. In: Abstracts, Symposium on the Biology and Management of Martens and Fishers. Ed. by S. W. Buskirk. Laramie: University of Wyoming. Pp. 89.
Zielinski, W. J.; Spencer, W. D.; Barrett, R. H. (1983): Relationship between food habits and activity patterns of pine martens. J. Mammalogy **64**, 387–396.

Author's address: Dr. Anthony P. Clevenger, Departamento de Biología Animal, Universidad de León, E-24071 León, Spain

Z. Säugetierkunde 58 (1993) 144–154

ISSN 0044-3468

Histologische Untersuchungen zur Entwicklung der Milchdrüse bei trächtigen Alpensteingeißen (*Capra i. ibex* L.)[1]

Von R. Weiss, M. Giacometti und H. Geyer

Veterinär-Anatomisches Institut der Universität Zürich und Zoologischer Garten Basel, Schweiz

Eingang des Ms. 17. 6. 1992
Annahme des Ms. 16. 11. 1992

Abstract

Histological observations on the development of mammary glands in Alpine ibex (Capra i. ibex L.) during pregnancy

On the basis of biopsy samples, the development of normal mammary glands of 29 alpine ibex (*Capra i. ibex* L.) during pregnancy were investigated histologically. The results were compared with well-known data of udder development of some domestic species, in particular of goats. Four different phases of udder development have been discerned.

The first phase, up to 10 weeks ante partum, is characterized by a non lactating mammary gland. In the second phase, 8 to 9 weeks ante partum, arborization of the lobular ducts and formation of true alveoli take place. In alpine ibex this occurs relatively late, shortly before the beginning of the last third of pregnancy. The third phase is initiated by the beginning of a sparse lipid secretion. The first lipid droplets appear at about 6 weeks ante partum. During the last phase, 4 weeks ante partum up to birth, strong secretion and accumulation of lipids are predominant.

The development of the udder in alpine ibex begins approximately one month later than in goats, and was observed to be more similar to the development of swine mammary glands.

Einleitung

Der Alpensteinbock (*Capra i. ibex* L.) ist heute im gesamten Alpenraum, von den Meeralpen im Westen bis zu den Steirischen Kalkalpen und den Karawanken im Osten, verbreitet. Der Bestand beträgt ca. 24 000 bis 28 000 Stück (Giacometti 1991b). Seit 1977 wird in der Schweiz unter strenger Kontrolle ein Teil der Steinbockkolonien zur Gesunderhaltung der Bestände und zur Verhinderung bzw. Minderung von Wildschäden wieder bejagt (Ratti 1986; Zingg 1988). Auch im Fürstentum Liechtenstein, in Österreich, Deutschland und Slowenien erfolgt eine Regulierung der Steinbockbestände durch die Jagd (Giacometti 1991b).

Der Wissensstand über das Steinwild war bis vor wenigen Jahren relativ gering. Deshalb wurde 1983 damit begonnen, ausgewählte Körpermaße und Organe von im Kanton Graubünden erlegten Tieren zu untersuchen und auszuwerten. An diesen Studien sind Hochschulinstitute in der Schweiz, in Österreich und Italien beteiligt. Ziel der vorliegenden Arbeit war es, den zeitlichen Ablauf der mikroskopischen Veränderungen an der Milchdrüse des Steinwildes während ihrer Entwicklung darzustellen, und sie mit jener der Haussäugetiere, insbesondere der Ziege, zu vergleichen. Zum besseren Verständnis der mikroskopischen Befunde an der Milchdrüse werden nachfolgend einige Aspekte der Biologie des Steinwildes, insbesondere der Reproduktionsbiologie, erläutert.

Das Steinwild bewohnt in erster Linie alpine Zonen, die über der Waldgrenze liegen. Nur im Frühjahr steigt es für kurze Zeit in tiefere Lagen ab, um das erste frische Grün zu äsen (Ratti 1986). Die Paarung findet in den Monaten Dezember und Januar statt. Die Steingeißen sind saisonal polyöstrisch. Die Zyklusdauer beträgt durchschnittlich 20 ± 1

[1] Herrn Prof. Dr. Josef Frewein zum 60. Geburtstag am 6. Februar 1993 gewidmet.

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5803-0144 $ 02.50/0

Tage (Stüwe und Grodinsky 1987; Giacometti 1991a). Nach einer mittleren Trächtigkeitsdauer von 167 ± 3 Tagen bringen die Steingeißen im Mai und Juni 1–2 Kitze zur Welt, wobei die meisten Geburten auf die erste Juniwoche fallen (Giacometti 1991a). Die Jungtiere werden ca. 6 Monate lang (bis zum Einsetzen der Brunft) gesäugt (Ratti 1986).

Material und Methode

Das Untersuchungsmaterial bestand aus den Milchdrüsen von 29 Steingeißen, die im Rahmen von Sonderabschüssen in den Monaten Dezember bis Juli der Jahre 1989–90 und 1990–91 erlegt worden sind (Tab. 1). Die Steingeissen stammten alle aus dem schweizerischen Teil der Kolonie Albris, die sich im Südosten des Kantons Graubünden, zwischen den Flüssen Spöl, Inn, Flazbach und dem oberen Teil des Poschiavino auf einer Fläche von ca. 240 km^2 erstreckt. Es kamen nur Milchdrüsen von Steingeißen zur Untersuchung, die zum Zeitpunkt des Abschusses nachweislich trächtig waren. Zwei Steingeißen wurden 5 bzw. 8 Wochen nach der Geburt der Kitze erlegt. Ihre Milchdrüsen dienten als Referenz für ein laktierendes Gesäuge.

Tabelle 1. **Daten der an der Milchdrüse untersuchten, trächtigen Alpensteingeißen und ihrer Foeten**

Nr.	Abschuss-datum	Alter Geiss in Monaten[1]	Gewicht Geiss in kg[2]	Alter Foetus in Tagen[3]	Gewicht Foetus in Gramm	Tage vor / nach Geburt[5]
1	25.1.90	55	25	k.A.[4]	k.A.	- 131[6]
2	12.1.90	139	29	33	0,058	- 130
3	19.2.90	92	34	49	3,77	- 118
4	19.2.90	176	28	57	14	- 110
5	22.2.90	57	22	65	34,5	- 102
6	28.2.90	93	22	k.A.	k.A.	- 97[6]
7	22.2.90	129	23	70	52	- 97
8	16.3.90	69	22	86	158	- 81
9	16.3.90	81	48	k.A.	k.A.	- 80[6]
10	16.3.90	57	22	k.A.	k.A.	- 80[6]
11	16.3.90	117	22	k.A.	k.A.	- 80[6]
12	16.3.90	189	22	88	176	- 79
13	4.4.90	58	15	90	196	- 77
14	16.3.90	105	22	90	202	- 77
15	4.4.90	154	26	96	272	- 71
16	4.4.90	70	21	106	416	- 61
17	4.4.90	58	20	109	469	- 58
18	4.4.90	142	26	109	480	- 58
19	3.5.91	60	18	126	874	- 41
20	3.5.91	96	21	140	1306	- 27
21	3.5.91	108	21	142	1408	- 25
22	28.5.90	48	18	146	1558	- 21
23	3.5.91	156	16	149	1670	- 18
24	19.6.90	96	26	149	1706	- 18
25	28.5.90	108	19	161	2286	- 6
26	28.5.91	170	19	164	1445	- 3
27	28.5.91	122	23	170	1790	0
28	14.7.90	145	27	-	-	+ 35
29	30.7.90	85	21	-	-	+ 56

[1] Alter zum Zeitpunkt des Abschusses; [2] Steingeiß aufgebrochen (mit Kopf und Fell, aber ohne Eingeweide); [3] Nach Hugget und Widdas (1951) errechnet; [4] Keine Angaben vorhanden; [5] Nach der Formel: Abschußdatum + (167 Tage – Alter des Foetus) errechnet; [6] Geschätzt aufgrund des Abschußdatums.

Die Gesäuge wurden durch die Wildhüter abgetrennt. Die Proben vom Jahr 1990 wurden bei −18 °C eingefroren und nach dem Eintreffen am Veterinär-Anatomischen Institut in 4 % Formalin aufgetaut und fixiert. Die Proben vom Jahr 1991 wurden direkt in 4 % Formalin eingelegt. Aus jedem der beiden Mammarkomplexe wurde ein kleiner Würfel mit einer Kantenlänge von 1 cm herausgeschnitten. Der eine Würfel stammte aus dem zitzennahen Bereich und der andere von der Euterbasis. Die Würfel wurden während mindestens 24 Stunden in Formol-Calzium nach Baker (Arnold 1968) bei 4 °C kühl aufbewahrt. Nach dem Einlegen im Gemisch nach Holt (1959) für 1–2 Stunden wurden sie bei −24 °C im Kryostat direkt eingefroren und geschnitten. Als Fettfärbungen für die ca. 10 μm dicken Gefrierschnitte dienten Sudan III und Fettrot 7B (Romeis 1989). Der ungeschnittene Rest der Gesäugewürfel wurde bis zur Weiterverarbeitung im Gemisch nach Holt (1959) aufbewahrt. Nach dem Entwässern in der Alkoholreihe, im Methylbenzoat und Xylol erfolgte ihre Einbettung in Paraffin. An den 7 μm dicken Paraffinschnitten wurden zur Beurteilung von Drüsen- und Bindegewebe die Färbungen Hämalaun-Eosin (HE), Alcianblau-PAS-Reaktion (pH 2,5) und Masson-Goldner (Romeis 1989) durchgeführt. Zur Bestimmung des prozentualen Flächenanteils von Drüsengewebe (Epithelzellen und Lumina der Alveolen) und Bindegewebe (intra- und interlobulär) wurden von jeder nach Masson-Goldner gefärbten Gewebsprobe nach dem Punktezählverfahren von Weibel (1979) 840 Punkte ausgezählt (Tab. 2). Die Zählung erfolgte mit der Strichplatte nach Weibel bei 200facher Vergrößerung.

Tabelle 2. **Prozentuale Verteilung der Gewebeteile in der Milchdrüse von Alpensteingeißen während der Entwicklung und nach der Geburt**

Nr.	Tage vor / nach der Geburt	Drüsengewebe in %	Epithel in %	Lumina in %	Bindegewebe in %	Intralobuläres Bindegewebe in %	Interlobuläres Bindegewebe in %
1	- 131	11,7	10,5	1,2	88,3	10,6	77,7
2	- 130	17,5	15,2	2,3	82,5	15,1	67,4
3	- 118	14,0	13,6	0,4	86,0	14,8	71,2
4	- 110	13,6	13,0	0,6	86,4	17,0	69,4
5	- 102	13,6	12,5	1,1	86,4	20,1	66,3
6	- 97	12,7	12,0	0,7	87,3	16,8	70,5
7	- 97	15,0	11,9	3,1	85,0	23,3	61,7
8	- 81	14,2	13,8	0,4	85,8	14,6	71,2
9	- 80	18,6	17,6	1,0	81,4	12,4	69,0
10	- 80	14,3	13,2	1,1	85,7	16,4	69,3
11	- 80	14,4	13,2	1,2	85,6	12,5	73,1
12	- 79	16,9	15,6	1,3	83,1	15,5	67,6
13	- 77	47,0	31,1	15,9	53,0	34,2	18,8
14	- 77	14,5	11,7	2,8	85,5	17,0	68,5
15	- 71	20,5	19,7	0,8	79,5	18,3	61,2
16	- 61	21,2	18,6	2,6	78,8	9,2	69,6
17	- 58	25,0	22,6	2,4	75,0	17,6	57,4
18	- 58	18,6	16,9	1,7	81,4	24,5	56,9
19	- 41	50,4	45,1	5,3	49,6	24,6	25,0
20	- 27	51,7	46,2	5,5	48,3	27,5	20,8
21	- 25	50,4	44,4	6,0	49,6	30,0	19,6
22	- 21	51,6	40,1	11,5	48,4	32,0	16,4
23	- 18	56,8	49,4	7,4	43,2	21,2	22,0
24	- 18	56,2	37,5	18,7	43,8	31,3	12,5
25	- 6	60,7	38,0	22,7	39,3	28,1	11,2
26	- 3	69,5	43,7	25,8	30,5	17,6	12,9
27	0	66,1	47,0	19,1	33,9	24,6	9,3
28	+ 35	65,0	45,8	19,2	35,0	21,9	13,1
29	+ 56	68,9	42,6	26,3	31,1	21,2	9,9

Ergebnisse

10 und mehr Wochen ante partum zeigen die Gewebeproben histologisch das Bild einer nicht laktierenden Milchdrüse. Das Eutergewebe besteht im Mittel aus allen untersuchten Proben (exkl. Steingeiß Nr. 13) zu 84,9 % aus Binde- und zu 15,1 % aus Drüsengewebe (Abb. 1, Tab. 3). 68,9 % des Bindegewebes liegen inter- und 16 % intralobulär. Beim Drüsengewebe entfallen 13,8 % auf das Epithel und 1,3 % auf das Lumen. Die kleinen Drüsenläppchen sind von breiten Bindegewebsbalken mit eingelagerten Fettzellgruppen umgeben (Abb. 2a). Die noch vorhandenen Epithelzellen bilden Ansammlungen ohne Lumen, oder sie sind zu kleinen Drüsenendstücken zusammengelagert (Abb. 2b, c). Die Lumina dieser Drüsenendstücke enthalten vielfach ein stark PAS-positives (rotes), serumähnliches Sekret, das sich im HE-Schnitt schwach eosinophil anfärbt. Sie sind vor allem an der Peripherie der Drüsenläppchen zu finden. Das einschichtige Epithel der Milchgänge besteht mehrheitlich aus platten bis kubischen Zellen (Abb. 2d). Dazwischen und unterhalb des Epithels sowie im intralobulären Bindegewebe liegen einzeln oder in kleinen Haufen angeordnet, mononukleäre Zellen (Lymphozyten, Plasmazellen und Makrophagen). Im intralobulären Bindegewebe befinden sich zusätzlich noch viele Mastzellen. Das

Tabelle 3. **Durchschnittlicher prozentualer Anteil der Gewebeteile in der Milchdrüse von Alpensteingeißen zu verschiedenen Zeiten vor und nach der Geburt**

Zeit in Wochen ante / post partum		> 10 a.p.	8 - 9 a.p.	6 a.p.	3 - 4 a.p.	0 - 1 a.p.	5 - 8 p.p.
Anzahl Tiere	n	14[1]	3	1	5	3	2
Drüsengewebe	x	15,1	21,6	50,4	53,3	65,4	67,0
	s	2,3	2,6	-	2,6	3,6	2,0
Epithel	x	13,8	19,4	45,1	43,5	42,9	44,2
	s	2,4	2,4	-	4,3	3,7	1,6
Lumina	x	1,3	2,2	5,3	9,8	22,5	22,8
	s	0,8	0,4	-	4,9	2,7	3,6
Bindegewebe	x	84,9	78,4	49,6	46,7	34,6	33,0
	s	2,3	2,6	-	2,6	3,6	2,0
Intralobuläres Bindegewebe	x	16,0	17,1	24,6	28,4	23,5	21,5
	s	3,1	6,3	-	3,9	4,4	0,4
Interlobuläres Bindegewebe	x	68,9	61,4	25,0	18,3	11,1	11,5
	s	4,1	5,9	-	3,4	1,5	1,6

[1] Ohne Steingeiß Nr. 13 (vgl. Text)

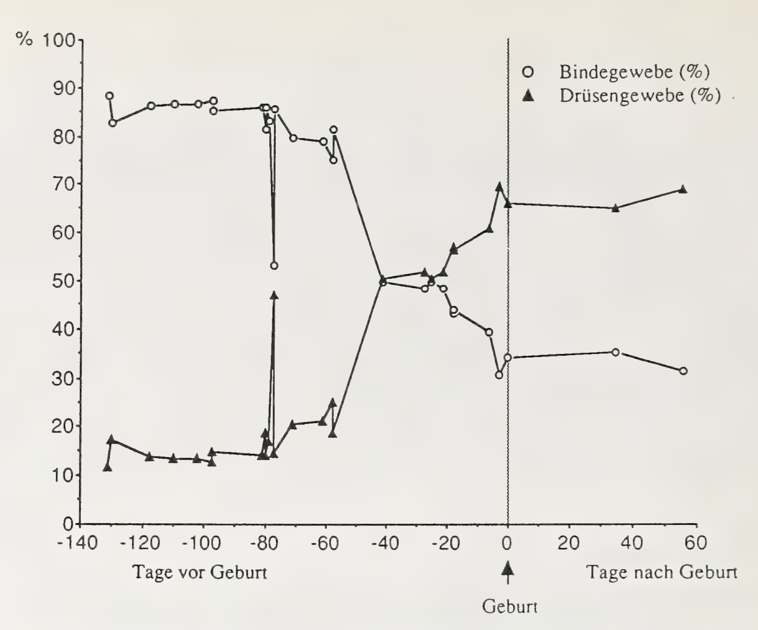


Abb. 1. Prozentualer Anteil des Drüsengewebes (Epithelzellen und Lumina der Alveolen) und des Bindegewebes (intra- und interlobulär) bei den ausgezählten Gewebsflächen der Milchdrüse der Alpensteingeiß vor und nach der Geburt

Abb. 2 (links). Milchdrüse einer Alpensteingeiß (Nr. 2), 130 Tage ante partum. Masson-Goldner. a = interlobuläres Bindegewebe, b = Drüsenepithelzellen, c = Drüsenendstück mit kleinem Lumen, d = Milchgangsepithel. – *Abb. 3 (rechts).* Milchdrüse einer Alpensteingeiß (Nr. 7), 97 Tage ante partum. Hämalaun-Eosin. a = Siegelringzellen der Rückbildung, b = mononukleäre Zellen im intralobulären Bindegewebe, c = interlobuläres Bindegewebe

Zytoplasma dieser großen, polymorphen Zellen ist mit kräftig gefärbten PAS-positiven und im HE-Schnitt basophilen Granula gefüllt. Der runde Zellkern liegt mehrheitlich exzentrisch. Er wird häufig von den zytoplasmatischen Granula verdeckt, so daß er kaum mehr zu erkennen ist. Bei den Steingeißen Nr. 5, 7 und 9 befinden sich noch Teile des Drüsengewebes in Rückbildung. Obwohl diese schon weit fortgeschritten ist, sind hauptsächlich an der Peripherie der Drüsenläppchen noch einzelne Siegelringzellen vorhanden (Abb. 3a). Ein weiteres Zeichen für die Rückbildung ist das vermehrte Auftreten von mononukleären Zellen im intralobulären Bindegewebe (Abb. 3b).

Die Eutergewebeproben der Steingeiß Nr. 13 zeigen lichtmikroskopisch das Bild einer Milchdrüse, die sich bereits in einer fortgeschrittenen Phase der Entwicklung befindet. Der Drüsengewebsanteil liegt bei 47 %, und auf das Bindegewebe entfallen 53 % (Abb. 1, Tab. 3). Dieses histologische Bild und die prozentuale Verteilung der ausgezählten Gewebeflächen treten bei der Steingeiß in der Regel erst 3 bis 4 Wochen ante partum auf.

8 bis 9 Wochen ante partum befindet sich die Milchdrüse der Steingeißen in der Phase der Proliferation der Ductus lactiferi und Entfaltung der alveolären Drüsenendstücke (Abb. 4a, b). Das Epithel der Drüsenendstücke ist höher geworden. Die isoprismatischen Zellen besitzen große, runde Zellkerne, die das Zellvolumen fast vollständig ausfüllen. Die Lumina der Drüsenendstücke sind noch sehr klein und teilweise mit dem unverändert homogenen, eosinophilen und stark PAS-positiven Sekret gefüllt. Das Epithel der Milchgänge ist ebenfalls kubisch, an manchen Stellen sogar zylindrisch (Abb. 4c). Im Interstitium fallen die zahlreich vorhandenen Plasmazellen auf. Der Drüsengewebsanteil hat sich

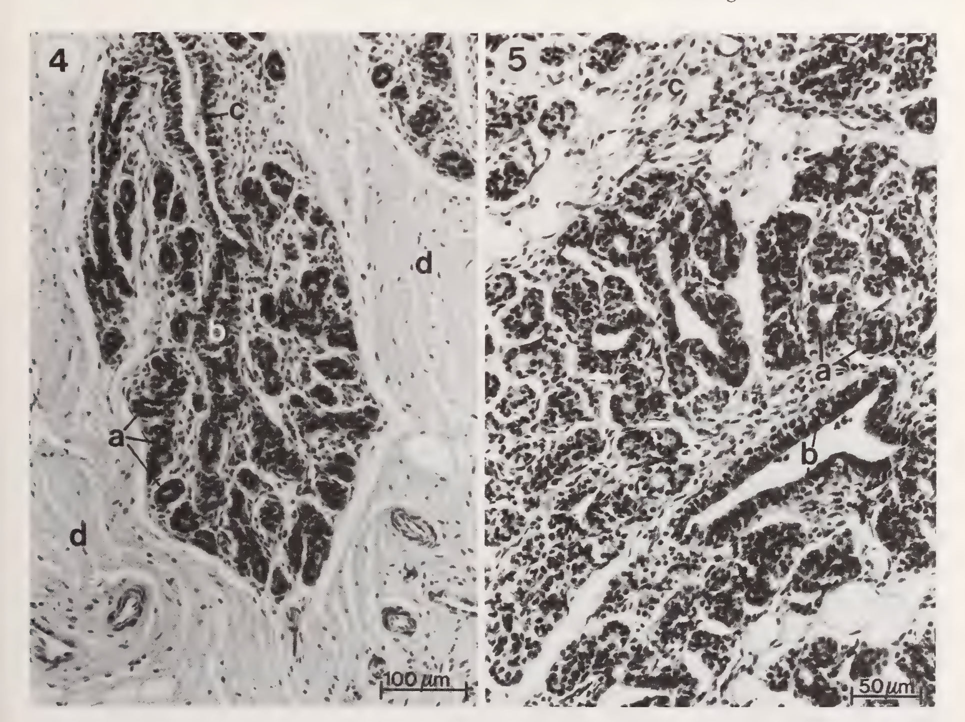


Abb. 4 (links). Milchdrüse einer Alpensteingeiß (Nr. 16), 61 Tage ante partum. Hämalaun-Eosin. Beginnende Proliferation der Ductus lactiferi und Entfaltung der Drüsenendstücke. a = Drüsenendstück mit kleinem Lumen, b = aussprossender Milchgang, c = Milchgangsepithel, d = interlobuläres Bindegewebe. – *Abb. 5 (rechts).* Milchdrüse einer Alpensteingeiß (Nr. 19), 41 Tage ante partum. Hämalaun-Eosin. a = Drüsenepithelzellen, b = Milchgangsepithel, c = interlobuläres Bindegewebe mit Fettzellen

leichtgradig auf durchschnittlich 21,6 % erhöht (Abb. 1, Tab. 3). Das Bindegewebe macht immer noch 78,4 % des Eutergewebes aus. 6 Wochen ante partum zeigen die Gewebeproben die ersten Anzeichen einer differenzierten Sekret(Milchfett-)bildung. Die ersten feinen Fetttröpfchen treten hauptsächlich lumenseitig auf. Die Zellkerne der Drüsenendstücke sind noch rund und liegen zentral. Das Epithel der Alveolen und Milchgänge ist hochprismatisch geworden (Abb. 5a, b). Bei der Mehrzahl der Alveolen ist ein mit Sekret gefülltes Lumen zu erkennen. Das stark eosinophile Sekret ist nur noch schwach PAS-positiv und färbt sich nach Masson-Goldner orange-rot an. Der Anteil des Drüsengewebes am Eutergewebe hat stark zugenommen. Er liegt nun bei 50,4 %, wobei das Epithel 45,1 % und die Lumina 5,3 % ausmachen (Abb. 1, Tab. 3). Der Bindegewebsanteil hat sich entsprechend auf 49,6 % verringert. Davon entfallen je etwa die Hälfte auf das intra- bzw. interlobuläre Bindegewebe.

3 bis 4 Wochen ante partum befinden sich die Milchdrüsen der Steingeißen in der Phase der starken Sekretion. Das neugebildete Fett wird anfänglich noch in den Epithelzellen zurückgehalten. Dieses großtropfige Fett füllt die Alveolarepithelzellen so stark aus, daß diese breite, apikale Fettsäume aufweisen, und die abgeflachten, teilweise mondsichelförmigen Zellkerne nach basal abgedrängt werden (Abb. 6a, b). Die mit großen Fetttropfen gefüllten Epithelzellen sind damit zu Siegelringzellen der Entwicklung geworden (Abb. 7a). Nach und nach erscheinen zuerst kleine und später auch große Fetttropfen im Lumen der Alveolen (Abb. 7c). Die Mehrzahl der Lumina ist mäßig weit. Der Durchmesser beträgt bereits 80 μm und mehr. Das Sekret hat sich kaum verändert. Der Drüsen-

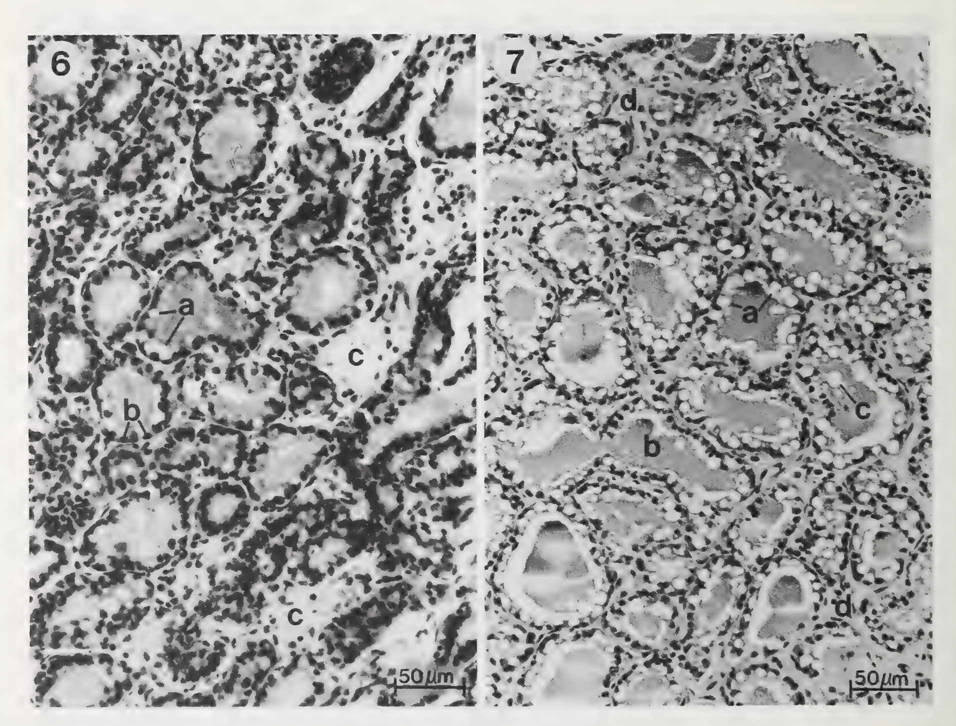


Abb. 6 (links). Milchdrüse einer Alpensteingeiß (Nr. 24), 18 Tage ante partum. Fettrot 7B. a = apikale Fettsäume, b = nach basal abgedrängte, mondsichelförmige Zellkerne, c = intralobuläres Bindegewebe. – *Abb. 7 (rechts).* Milchdrüse einer Alpensteingeiß (Nr. 26), 3 Tage ante partum. Hämalaun-Eosin. a = prall mit Fett gefüllte Epithelzellen = Siegelringzellen der Entwicklung, b = Sekret mit feinen Granula, c = große intraluminale Lipidvokuolen, d = intralobuläres Bindegewebe

gewebsanteil ist noch einmal leicht angestiegen und beträgt im Mittel 53,3 % (Abb. 1, Tab. 3). Der Anteil des Bindegewebes liegt bei 46,7 %. In der letzten Woche ante partum sind die Alveolen sehr weit (Abb. 7). Ihr Durchmesser beträgt durchschnittlich 100–200 µm. Die meisten Epithelzellen sind prall mit Fett gefüllt (Abb. 7a). Das vorerst nur mäßig fetthaltige, feinkörnige Sekret (Abb. 7b) ist PAS-negativ geworden und färbt sich nach Masson-Goldner grau-grün an. Erst kurz vor der Geburt ist das Lumen der Alveolen fast vollständig mit großtropfigem Fett ausgefüllt (Abb. 8a). Das Drüsengewebe macht kurz vor der Geburt durchschnittlich 65,4 % des Eutergewebes aus (Abb. 1, Tab. 3). 42,9 % der ausgezählten Gewebefläche werden vom Epithel und 22,5 % von den Lumina eingenommen. Der Anteil des Bindegewebes ist auf 34,6 % abgesunken. Davon entfallen 11,1 % auf das inter- und 23,5 % auf das intralobuläre Bindegewebe.

An der laktierenden Milchdrüse, 5 bzw. 8 Wochen post partum, nimmt das Drüsengewebe im Mittel 67 % und das Bindegewebe 33 % der Fläche ein (Abb. 1, Tab. 3). Beim Drüsengewebe entfallen 44,2 % auf das Epithel und 22,8 % auf die Lumina der Alveolen. Beim Bindegewebe liegen 21,5 % intra- und 11,5 % interlobulär. Die Alveolen sind unterschiedlich weit. Die Mehrzahl von ihnen besitzt ein hochprismatisches Epithel, dessen Zellen sich als Zeichen der aktiven Sekretabgabe ins Lumen vorwölben (Abb. 9a). Die großen Epithelzellen enthalten feine Fetttröpfchen im Zytoplasma (Abb. 9b). Ein kleiner Teil der Alveolen ist stark dilatiert und von einem flachen kubischen Epithel ausgekleidet. Im intralobulären Bindegewebe sind stellenweise viele mononukleäre Zellen vorhanden, die vorwiegend aus Lymphozyten und Plasmazellen bestehen (Abb. 9c).

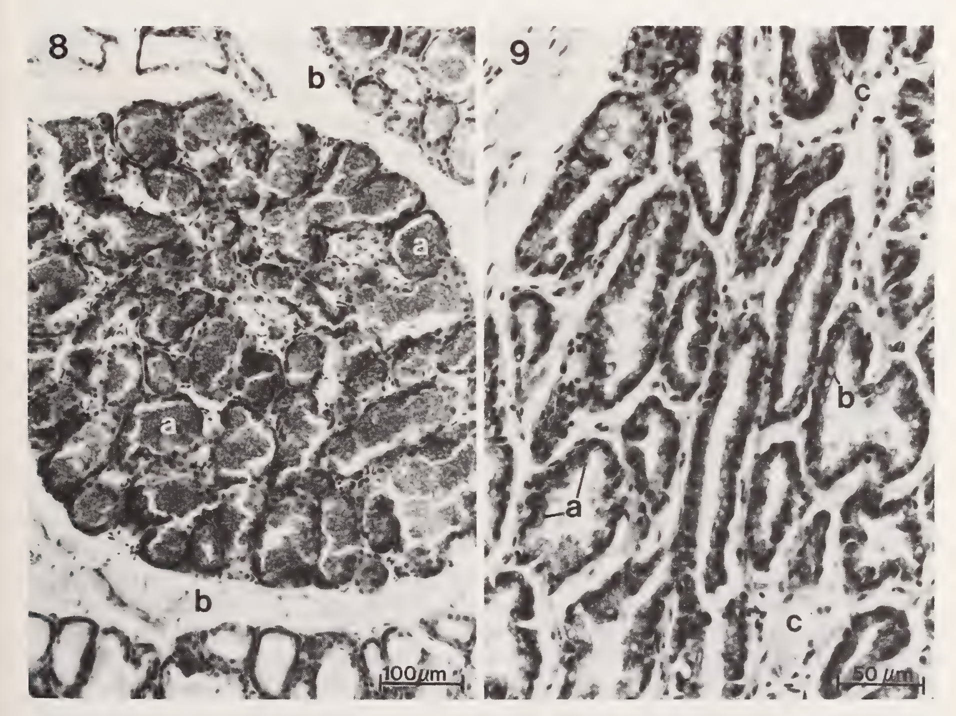


Abb. 8 (links). Milchdrüse einer Alpensteingeiß (Nr. 26), 3 Tage ante partum. Sudan III. Die Lumina der Alveolen sind vollständig mit großtropfigem Fett gefüllt. a = mit Fett gefüllte Alveolen, b = interlobuläres Bindegewebe. – *Abb. 9 (rechts).* Laktierende Milchdrüse einer Alpensteingeiß (Nr. 28), 5 Wochen post partum. Hämalaun-Eosin. a = Epithelzellen mit lumenseitiger Vorwölbung als Zeichen aktiver Milchsekretion, b = Fetttröpfchen im Zytoplasma, c = intralobuläres Bindegewebe mit vereinzelten Lymphozyten und Plasmazellen

Diskussion

Durch die Aneinanderreihung von histologischen Erscheinungsbildern wurde an Gewebeproben versucht, den zeitlichen Ablauf der Entwicklung der Milchdrüse bei trächtigen Steingeißen (*Capra i. ibex* L.) zu gliedern. Dabei lassen sich vier Phasen unterscheiden. Da die einzelnen Phasen fließend ineinander übergehen, wurde die Zäsur zwischen den einzelnen Phasen dort gesetzt, wo markante histologische Veränderungen erstmals auftreten.

Eine besonders markante Veränderung im histologischen Bild ist 6 Wochen ante partum zu beobachten, wenn sich lichtmikroskopisch die ersten feinen Fetttröpfchen in den Drüsenepithelzellen nachweisen lassen. Zu dieser Zeit (Mitte bis Ende April) beginnt in den Bergen der Frühling (Godli 1992) und die Alpensteinböcke steigen in tiefere Regionen unterhalb der Waldgrenze hinab, um das erste frische Grün zu äsen (Ratti 1986; Zingg 1988). Während der Wintermonate bilden rohproteinarme Gräser, Zwergsträucher, Nadelgehölze und Flechten ihre Nahrungsgrundlage (Tataruch et al. 1991). Das verbesserte, rohprotein- und energiereiche Nahrungsangebot im Frühling, mit frischen Gräsern und Laubgehölzen, spielt wahrscheinlich für den Beginn der Milchfettbildung eine entscheidende Rolle.

Die Entwicklung der Milchdrüse während der Gravidität verläuft bei Säugetieren nicht immer einheitlich. Bei C_3H/HeN Mäusen beispielsweise, stehen in der ersten Trächtigkeitshälfte nur ca. 50 % der Alveolen auf der gleichen Entwicklungsstufe (Mills und Topper 1970). Hörnlimann (1988) stellte bei der Milchdrüse von Veredelten Landschweinen und Edelschweinen im ersten Drittel der Trächtigkeit ebenfalls erhebliche Unterschiede im Entwicklungszustand fest. Unsere Untersuchungen zeigen bei den Steingeißen eine ähnliche Tendenz. Im gleichen Euter sind immer Drüsenbezirke vorhanden, die in ihrer Entwicklung vom durchschnittlichen Gesamtbild abweichen. Große Unterschiede im zeitlichen Ablauf der Milchdrüsenentwicklung sind auch zwischen den einzelnen Steingeißen zu beobachten. Das zeigen die Gewebeproben der Steingeiß Nr. 13 (Tab. 2). Bereits 11 Wochen vor der zu erwartenden Geburt befindet sich ihre Milchdrüse in einem fortgeschrittenen Stadium der Entwicklung, das bei allen anderen untersuchten tragenden Steingeißen in der Regel erst ab der 4. Woche ante partum gefunden wird.

Stammesgeschichtlich betrachtet, sind alle bei uns gehaltenen Ziegenrassen mit dem Alpensteinbock sehr nahe verwandt (Grzimek und Nievergelt 1968) und gehören derselben Gattung (*Capra*) an. In menschlicher Obhut pflanzen sie sich untereinander fort und erzeugen fruchtbare Bastarde (Couturier 1962). Mit einer Graviditätsdauer von durchschnittlich 150 und 167 Tagen, weisen Hausziegen und Steingeißen vergleichbare Werte auf. Trotz der nahen Verwandtschaft bestehen gewisse Unterschiede im zeitlichen Ablauf der Entwicklungsvorgänge der Milchdrüse. Die Entwicklung des Ziegeneuters wurde von Turner und Gomez (1936) bei Toggenburgerziegen und von Bentivoglio (1985) bei Saanenziegen und Gemsfarbigen Gebirgsziegen eingehend untersucht. Bentivoglio (1985) unterteilte die Entwicklung in eine Frühphase (bis 85 Tage ante partum), in eine Phase der Alveolenbildung mit beginnender Sekretion (85–30 Tage ante partum) und in eine Phase der starken Sekretion und Sekretstauung (ab 30. Tag ante partum). Die Entwicklung des Euters dauert bei primi- und pluriparen Ziegen insgesamt ca. 3 Monate, d. h. etwa einen Monat länger als bei der Steingeiß. Zwei Monate vor der Geburt sind bei allen Ziegen bereits deutliche Zeichen der Sekretion in Form von Fetttröpfchen zu sehen. Bei Steingeißen beginnt die Phase der Sekretion erst 1½ Monate ante partum. Ein Grund für diese Differenzen im zeitlichen Ablauf der Milchdrüsenentwicklung dürfte unter anderem im Futterangebot während der Gravidität zu suchen sein. Hausziegen haben auch in den Wintermonaten immer wieder Zugang zu energie- und proteinreichem Futter und weisen im Vergleich zu Wildwiederkäuern auch eine deutlich höhere Milchleistung auf.

Ziegler und Mosimann (1960) unterschieden bei der Entwicklung der Milchdrüse des

Rindes in der ersten Trächtigkeit ebenfalls drei Phasen. Die erste Phase (1.–3. Trächtigkeitsmonat) war geprägt von der Proliferation der Sammel- und Ausführungsgänge. In der zweiten Phase (4.–7. Trächtigkeitsmonat) entfalteten sich die Alveolen und die Sekretion begann. Die letzte Phase (ab 8. Trächtigkeitsmonat) stand ganz im Zeichen der Sekretion. Obwohl die Entwicklung der Milchdrüse bei Rindern länger als bei Ziegen dauert, beginnt bei beiden Haustierformen die Sekretionsphase knapp vor der Graviditätsmitte.

Beim Veredelten Landschwein verläuft die Entwicklung der Milchdrüse sehr rasch (Giese 1985). Giese (1985) unterteilte die Entwicklung der Schweinemilchdrüse in eine Phase der Milchgangsproliferation (bis ca. 6 Wochen ante partum), in eine Phase der Alveolenbildung mit Synthese sowie Abgabe von wenig homogenem eosinophilen Sekret in das Lumen (ab 6. Woche ante partum), in eine Phase der differenzierten Sekretbildung mit schwacher Sekretion (ab 4. Woche ante partum) und in eine Phase der starken Sekretion mit Sekretstauung (ab 2. Woche ante partum). Wie bei der Milchdrüse von Steingeißen erfolgt auch bei Schweinen die Bildung von differenziertem Sekret mit Beginn des letzten Viertels der Trächtigkeit. Die pluriparen Schweine setzen wesentlich später mit der Entwicklung der Milchdrüse ein, durchlaufen diese aber rascher. Bei zum 4. mal trächtigen Sauen beispielsweise, beginnt die Sekretion erst 2 Wochen vor der Geburt (Giese 1985).

Danksagung

Ein besonderer Dank gilt Dr. P. Ratti vom Jagd- und Fischereiinspektorat des Kantons Graubünden, den Wildhütern D. Godli, J. Schaniel und A. Plozza für ihre wohlwollende Unterstützung dieser Arbeit, Frau A. Hulftegger für die Herstellung der histologischen Schnitte und Frau J. Peter für die Hilfe bei den graphischen Arbeiten.

Zusammenfassung

An Gewebeproben von normalen Milchdrüsen von 29 trächtigen Steingeißen (*Capra i. ibex* L.) wurde der zeitliche Verlauf der Entwicklung histologisch untersucht und mit dem unserer Haussäugetiere, insbesondere der Ziege, verglichen. Die Entwicklung der Milchdrüse der Steingeiß kann in vier Phasen unterteilt werden. Bis 10 Wochen ante partum zeigen die Gewebeproben das histologische Bild einer ruhenden, nicht laktierenden Milchdrüse. Die zweite Phase beginnt 8–9 Wochen ante partum und ist gekennzeichnet durch die Aussprossung der Milchgänge und Entfaltung der Drüsenendstücke. Letztere setzt als Vorbereitung auf die Laktation bei der Steingeiß relativ spät, nämlich erst kurz vor dem Beginn des letzten Drittels der Trächtigkeit, ein. Die dritte Phase ist durch die beginnende, differenzierte Sekretbildung und schwache Sekretion charakterisiert. Der lichtmikroskopische Nachweis von Lipidtröpfchen im Alveolarepithel, gelingt erst ab der 6. Woche ante partum. In der letzten Phase (ab 4. Woche ante partum) stehen die starke Sekretion und Sekretstauung im Vordergrund. Die Entwicklung der Milchdrüse beginnt bei Steingeißen etwa einen Monat später als bei Ziegen und entspricht in ihrem zeitlichen Ablauf vielmehr dem der Schweinemilchdrüse.

Literatur

Arnold, M. (1968): Histochemie. Einführung in Grundlagen und Prinzipien der Methoden. Berlin, Heidelberg, New York: Springer Verlag.

Bentivoglio, F. (1985): Histologische und histochemische Untersuchungen zur Anbildung der Milchdrüse bei trächtigen Ziegen. Vet. Med. Diss., Zürich.

Couturier, M. A. J. (1962): Le bouquetin des alpes. Edition par l'auteur, Grenoble.

Giacometti, M. (1991a): Primi risultati di un'indagine sulla riproduzione e dinamica di popolazione nello stambecco della colonia dell'Albris (Grigioni, Svizzera). In: Notiziario del Gruppo Stambecco Europa. No. 4. Edizione Parco Nazionale Gran Paradiso, Torino (im Druck).

— (1991b): Beitrag zur Ansiedlungsdynamik und aktuellen Verbreitung des Alpensteinbockes (*Capra i. ibex* L.) im Alpenraum. Z. Jagdwiss. **37**, 157–173.

Giese, L. (1985): Histologische und histochemische Untersuchungen an der Milchdrüse der Sau während der Anbildung im letzten Drittel der Trächtigkeit. Vet. Med. Diss., Zürich.

Godli, D. (1992): Wildhüter im Albris-Gebiet, Pontresina (CH). (Pers. Mit.).

Grzimek, B.; Nievergelt, B. (1968): Ziegen und Schafe. In: Grzimeks Tierleben. Enzyklopädie des Tierreiches. Hersg. von B. Grzimek, Zürich: Kindler Verlag. Bd. **XIII**, 518–521.

Hörnlimann, B. (1988): Histologische Untersuchungen zur prä- und postnatalen Entwicklung der Milchdrüse beim weiblichen und männlichen Schwein. Vet. Med. Diss., Zürich.
Holt, S. J. (1959): Factors governing the validity of staining methods for enzymes, and their bearing upon the Gomori acid phosphatase technique. Exp. Cell Res. Suppl. **7**, 1–27.
Huggett, A. St G.; Widdas, W. F. (1951): The relationship between mammalian foetal weight and conception age. J. Physiol. **114**, 306–317.
Mills, E. S.; Topper, Y. J. (1970): Some ultrastructural effects of insulin, hydrocortisone, and prolactin on mammary gland explants. J. Cell Biol. **44**, 310–328.
Ratti, P. (1986): Leitfaden für Bündner Jäger. Jagd- und Fischereiinspektorat des Kantons Graubünden, Chur. S. 21–31.
Romeis, B. (1989): Mikroskopische Technik. 17. Aufl. München, Wien, Baltimore: Urban und Schwarzenberg.
Stüwe, M.; Grodinsky, C. (1987): Reproductive biology of captive alpine ibex (*Capra i. ibex*). Zoo Biology **6**, 331–339.
Tataruch, F.; Steineck, T.; Klansek, E.; Vavra, I.; Ratti, P.; Giacometti, M. (1991): Untersuchungen an Steinwild aus Graubünden (Schweiz). I. Analysen der Nahrungszusammensetzung, der Aktivität der Schilddrüsen und Nebennieren sowie der Reproduktion. Wien. tierärztl. Mschr. **78**, 351–356.
Turner, C. W.; Gomez, E. T. (1936): The development of the mammary glands of the goat. Mo. Agr. Exp. Sta. Res. Bull. **240**.
Weibel, E. R. (1979): Stereological methods. London, New York: Academic Press. Vol. 1.
Ziegler, H.; Mosimann, W. (1960): Anatomie und Physiologie der Rindermilchdrüse. Berlin, Hamburg: Paul Parey.
Zingg, R. (1988): Alpensteinbock (*Capra ibex ibex*). In: Grzimeks Enzyklopädie. Hrsg. von B. Grzimek. München: Kindler Verlag. Bd **5**, 516–523.

Anschriften der Verfasser: Dr. med. vet. Roger Weiss, Prof. Dr. med. vet. Hans Geyer, Veterinär-Anatomisches Institut, Winterthurerstr. 260, CH-8057 Zürich; Dr. med. vet. Marco Giacometti, Zoologischer Garten, CH-4054 Basel, Schweiz

Z. Säugetierkunde 58 (1993) 155–159

ISSN 0044-3468

Lack of genetic transferrin variation in European roe deer (*Capreolus capreolus* Linné)

By S. Herzog, Christine Mushövel, and A. Herzog

Receipt of Ms. 20. 7. 1992
Acceptance of Ms. 4. 12. 1992

Abstract

A study of transferrin in four different roe deer (*Capreolus capreolus*) populations from Central Europe has revealed a lack of genetic variation of this protein system. Some possible explanations of this phenomenon are discussed. It is assumed that the monomorphism of this protein system in roe deer is the consequence of selection rather than of genetic drift.

Introduction

During the last decade, deer (Cervidae) became one of the most intensively studied family with respect to their protein variability. However, roe deer (*Capreolus capreolus* Linné) as the most common deer species in Europe has been neglected. The first major study on biochemical variation of this species was that of Hartl and Reimoser (1988) on five populations from Austria, including 27 isoenzyme systems. The transferrin gene locus that has turned out to be the most differentiation relevant protein system within other cervid species such as red deer (*Cervus elaphus*, Herzog et al. 1991) was not covered by this study. Transferrin has been shown to be one of the most variable protein systems within animal species in general (Selander 1976). Among the Cervidae, transferrin variability shows a wide range between the species.

Transferrin is quite variable in European red deer (*Cervus elaphus*; McDougall and Lowe 1968; Kravchenko and Kravchenko 1971; Bergmann 1976; Gyllensten et al. 1980; Gyllensten et al. 1983; Herzog 1988; Herzog et al. 1991), white-tailed deer (*Odocoileus virginianus*; Miller et al. 1965; Manlove et al. 1975; Ramsey et al. 1979; Breshears et al. 1988) and especially in reindeer (*Rangifer tarandus*; Brænd 1964; Shubin 1969; Røed 1985, 1986, 1987). On the other hand, the American wapiti (*Cervus elaphus canadensis*; only one population studied by Cameron and Vyse 1978), sika deer (*Cervus nippon nippon*; only one park population of unknown origin studied by McDougall and Lowe 1968) as well as several fallow deer populations (*Cervus dama*; McDougall and Lowe 1968; Pemberton and Smith 1985; Hartl et al. 1986) studied to date were found to be monomorphic. However, studies by Herzog (1988, 1989) revealed that other fallow deer populations have maintained a certain degree of transferrin variation.

Roe deer already showed a lack of transferrin variation in a first study of altogether 33 animals from three sampling sites in Sweden (Gyllensten et al. 1980). However, it could be assumed that the lack of genetic variation was due to the restricted number of individuals studied. Such a phenomenon had been shown also for the moose (*Alces alces*): Whereas early studies on animals from North America (Nadler et al. 1967), Russia (Shubin 1969) and Scandinavia (Brænd 1962; Wilhelmson et al. 1978) found no genetic transferrin variation, a more extensive investigation found two different alleles (Gyllensten et al. 1980).

Thus, a study of a larger sample of roe deer from Central Europe was initiated in order to evaluate the level of transferrin variability within these Central European populations.

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5803-0155 $ 02.50/0

Material and methods

A total of 128 roe deer from four sites of the Central European population have been studied: 18 animals from Niedersachsen (Lüneburger Heide), 58 animals from Hessen, 28 animals from Rheinland-Pfalz and 24 animals from Baden-Württemberg. Figure 1 shows the sampling sites.

Blood samples of 10 ml were taken from the Vena cava immediately post mortem into heparinized tubes and kept under refrigeration during transport. The processing of the samples, separation by horizontal isoelectric focussing in polyacrylamide gels and by electrophoresis in starch gels, as well as the staining procedure followed Mushövel (1986) and Herzog (1988, 1991). Transferrin bands were identified by ^{59}Fe autoradiography.



Fig. 1. Map of sampling sites: L = Lüneburger Heide, Niedersachsen, H = Hessen, R = Rheinland-Pfalz, B = Baden-Württemberg

Results and discussion

No phenotypic variation of transferrin was found either within or between the four subpopulations. The single observed phenotype is shown in Figure 2.

The association of the protein bands leads us to the hypothesis of genetic control by one gene locus, as has been observed for other Artiodactyla and especially Cervidae. A formal genetic analysis was prohibited by the lack of variation.

The results are surprising insofar as the study of Hartl and Reimoser (1988) revealed a relatively high level of genetic variability. They found an average heterozygosity ranging between 3.5 % and 7.9 % for 161 animals from five populations under the assumption of 41 controlling gene loci. Including the data of Gyllensten et al. (1980), we have to assume that European roe deer shows only a minimal level or even a lack of transferrin variation.

Studies on cervid species often argued that bottleneck effects may be responsible for the lack of genetic variation. This would not be the case for roe deer due to the lack of isolating situations during the more recent past as well as due to the relatively high level of protein variation found by Hartl and Reimoser (1988): Bottleneck effects should act on all genetic loci simultaneously.

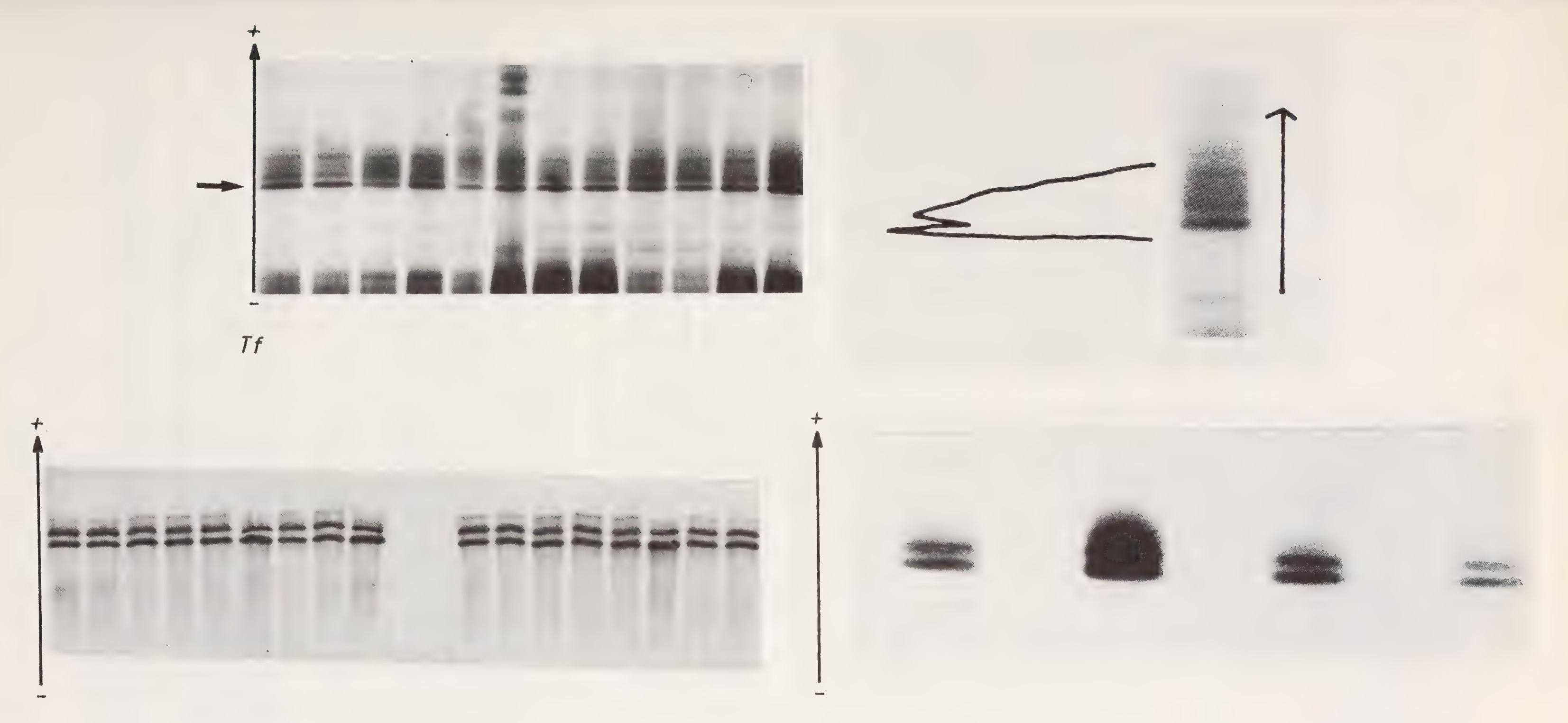


Fig. 2. Transferrin phenotype observed in this study. *a (above left):* Isoelectric focussing in polyacrylamide gels; *b (above right):* Densitometry of the transferrin pattern; *c (below left):* Double-one dimensional electrophoresis of transferrin; *d (below right):* Autoradiography of transferrin in the electropherogram

Among Cervidae, significant deficiencies of heterozygotes relative to Hardy-Weinberg proportions have been found in a number of wild red deer populations. GYLLENSTEN et al. (1980) observed such a deficiency in one population. These authors assumed a Wahlund effect to be the reason for this phenomenon. However, a Wahlund effect would also act on all genetic loci and not only on one single locus. The findings of SCHREIBER et al. (1992) show a significant deficiency of heterozygotes within a red deer population from Vosges du Nord.

Thus, we have to look for studies on mechanisms shaping the transferrin polymorphism. Whereas such data are completely lacking for roe deer, some indications are found for other cervids, especially red deer and reindeer. PEMBERTON et al. (1988) found a correlation between isozyme and transferrin variation on the one hand and juvenile survival in red deer on the other. For the Cervidae, experiments on the impact of transferrin on components of fitness are still lacking. However, for cattle (*Bos taurus*) there is good evidence for selection against certain heterozygous transferrin types (for review see BUSCHMANN and SCHMID 1968). This leads us to the hypothesis that selection against certain, especially heterozygous transferrin types has to be discussed as an important factor causing deficiencies of heterozygotes or even monomorphism at least between the adult individuals.

Another question to be discussed here is the validity of a hypothesis of HARRINGTON (1985). This author assumes that the *r*-selected roe deer could be expected to be genetically less variable than *K*-"strategists" among the Cervidae as e.g. the red deer. The present data would give support to this hypothesis when recognizing only the transferrin gene locus. On the other hand, the average heterozygosity calculated over a number of presumptive gene loci (HARTL and REIMOSER 1988) are a strong argument against this idea, even in view of the lack of genetic analysis in this study. Moreover, for roe deer the environment should appear to be more "coarse-grained" than for, say, red deer. A synopsis of the previous ideas, i.e. the "environmental grain"-hypothesis (SELANDER and KAUFMAN 1973) as well as the assumption that generalist species are genetically more variable than specialists (NEVO 1978) leads to a non-uniform picture. The actual state of our knowledge is that factors preventing the loss of genetic variation as e.g. a lack of bottleneck situations may overlay a potential tendency towards reduced genetic variation. This would also explain the phenomenon, that selection-relevant genetic loci as the transferrin may become fixed for a single allele, whereas the genetic variability in general is maintained on a relatively high level.

Zusammenfassung

Keine genetische Variation des Transferrins beim Europäischen Reh (Capreolus capreolus Linné)

Eine Untersuchung des Transferrins in vier verschiedenen mitteleuropäischen Rehwildpopulationen (*Capreolus capreolus*) ergab keinerlei genetische Variation dieses Proteinsystems. Einige mögliche Erklärungen für dieses Phänomen werden diskutiert. Es ist anzunehmen, daß der Monomorphismus in Bezug auf dieses Proteinsystem beim Rehwild eine Folge von Selektion und nicht von genetischer Drift ist.

References

BERGMANN, F. (1976): Beiträge zur Kenntnis der Infrastrukturen beim Rotwild. Teil II. Erste Versuche zur Klärung der genetischen Struktur von Rotwildpopulationen an Hand von Serumprotein-Polymorphismen. Z. Jagdwiss. **22**, 28–35.

BUSCHMANN, H.; SCHMID, D. O. (1968): Serumgruppen bei Tieren. Berlin, Hamburg: Verlag Paul Parey.

BRÆND, M. (1962): Studies on blood and serum groups in the elk (*Alces alces*). Ann. N.Y. Acad. Sci. **97**, 296–305.

BRÆND, M. (1964): Polymorphismus in the serum proteins of the reindeer. Nature **203**, 674.

BRESHEARS, D. D.; SMITH, M. H.; COTHRAN, E. G.; JOHNS, P. E. (1988): Genetic variability in white-tailed deer. Heredity **60**, 139–146.

Cameron, D. G.; Vyse, E. R. (1978): Heterozygosity in Yellowstone Park elk, *Cervus canadensis*. Biochemical Genetics **16**, 651–657.

Gyllensten, U.; Reuterwall, C.; Ryman, N.; Ståhl, P. (1980): Geographical variation of transferrin allele frequencies in three deer species from Scandinavia. Hereditas **92**, 237–241.

Gyllensten, U.; Ryman, N.; Reuterwall, C.; Dratch, P. (1983): Genetic differentiation in four European subspecies of red deer (*Cervus elaphus* L.). Heredity **51**, 561–580.

Hartl, G. B.; Reimoser, F. (1988): Biochemical variation in roe deer (*Capreolus capreolus* L.): are *r*-strategists among deer genetically less variable than *K*-strategists? Heredity **60**, 221–227.

Hartl, G. B.; Schleger, A.; Slowak, M. (1988): Genetic variability in fallow deer, *Dama dama* L. Animal Genetics **17**, 335–341.

Herzog, S. (1988): Cytogenetische und biochemisch-genetische Untersuchungen an Hirschen der Gattung *Cervus* (Cervidae, Artiodactyla, Mammalia). Göttingen Research Notes in Forest Genetics **10**, 1–139.

— (1989): Genetic polymorphism of transferrin in fallow deer, *Cervus dama* L. Animal Genetics **20**, 421–426.

Herzog, S.; Mushövel, C.; Hattemer, H.; Herzog, A. (1991): Transferrin polymorphism and genetic differentiation in *Cervus elaphus* L. (European red deer) populations. Heredity **67**, 231–239.

McDougall, E. I.; Lowe, V. P. (1968): Transferrin polymorphism and serum proteins of some British deer. J. Zool. (London) **155**, 131–140.

Manlove, M. N.; Avise, J. C.; Hillestad, H. O.; Ramsey, P. R.; Smith, M. H.; Straney, D. O. (1975): Starch gel electrophoresis for the study of population genetics in white-tailed deer. Proc. Annual Conf. South-Eastern Associ. Game and Fish Commissioners, New Orleans. Pp. 392–403.

Miller, W. J.; Haugen, A. O.; Roslien, D. J. (1965): Natural variation in the blood proteins of white-tailed deer. J. Wildl. Manage. **29**, 717–722.

Nadler, C. F.; Hughes, C. E.; Harris, K. E.; Nadler, N. W. (1967): Electrophoresis of the serum proteins and transferrins of *Alces alces* (elk), *Rangifer tarandus* (reindeer), and *Ovis dalli* (dall sheep) from North America. Comp. Biochem. Physiol. **23**, 149–157.

Nevo, E. (1978): Genetic variation in natural populations: patterns and theory. Theor. Pop. Biol. **13**, 121–177.

Pemberton, J. M.; Albon, S. D.; Guiness, F. E.; Clutton-Brock, T. H.; Berry, R. J. (1988): Genetic variation and juvenile survival in deer. Evolution **42**, 921–934.

Pemberton, J. M.; Smith, R. H. (1985): Lack of biochemical polymorphism in British fallow deer. Heredity **55**, 199–207.

Ramsey, P. R.; Avise, J. C.; Smith, M. H.; Urbston, D. F. (1979): Biochemical variation and genetic heterogeneity in South Carolina deer populations. J. Wildl. Manage. **43**, 136–142.

Røed, K. H. (1985): Genetic differences at the transferrin locus in Norwegian semi-domestic and wild reindeer (*Rangifer tarandus* L.). Hereditas **102**, 199–206.

— (1986): Genetic variability in Norwegian wild reindeer (*Rangifer tarandus* L.). Hereditas **104**, 293–298.

— (1987): Transferrin variation and body size in reindeer, *Rangifer tarandus* L. Hereditas **106**, 67–71.

Schreiber, A.; Klein, F.; Lang, G. (1992): Deficiency of heterozygotes at the transferrin locus in an autochthonous population of Central European red deer. In: Ongulés / Ungulates 91. Ed. by F. Spitz, G. Janeau, G. Gonzales, and S. Aulagnier. Paris, Toulouse: SFEPM-IRGM. Pp. 117–122.

Selander, R. K. (1976): Genic variation in natural populations. In: Molecular Evolution. Ed. by F. J. Ayala. Sunderland: Sinauer Ass.

Selander, R. K.; Kaufman, D. W. (1973): Genetic variability and strategies of adaptation in animals. Proceed. Nat. Acad. Sciences U.S.A. **70**, 1875–1877.

Shubin, P. N. (1969): The genetics of transferrin in the reindeer and in the European elk. Genetika **5**, 37–41.

Wilhelmson, M.; Juneja, R. K.; Bengtsson, S. (1978): Lack of polymorphism in certain blood proteins and enzymes of European and Canadian moose (*Alces alces*). Naturaliste Can. **105**, 445–449.

Authors' addresses: Dr. Sven Herzog, Abt. Forstgenetik und Forstpflanzenzüchtung, Georg-August-Universität, Büsgenweg 2, D-37077 Göttingen; Dr. Christine Mushövel, and Prof. Dr. Alexander Herzog, Fachgebiet Veterinärmedizinische Genetik und Zytogenetik, Justus-Liebig-Universität, Hofmannstraße 10, D-35392 Gießen, Germany

Z. Säugetierkunde 58 (1993) 160–171

ISSN 0044-3468

Dispersion and habitat preference of the Water vole *(Arvicola terrestris)* on the River Thames

By P. F. Woodall

Animal Ecology Research Group, Department of Zoology, University of Oxford, Oxford, England

Receipt of Ms. 13. 10. 1992
Acceptance of Ms. 12. 11. 1992

Abstract

Investigated the dispersion of water voles *(Arvicola terrestris)* over a two year period on a 1.6 km stretch of the River Thames near Oxford, England. Dispersion was significantly clumped, most pronounced for adult females, followed by juveniles and least for adult males. The river bank was divided in 32 50-metre sections and data on the vegetation and physical features of each section were analysed with the frequency of water vole catches in each section to determine habitat preferences. Water vole catches were positively correlated with water depth, *Urtica, Phragmites,* and short unidentified grasses and negatively correlated with bank height, bank depth, *Polygonum, Phalaris, Sparganium, Juncus.* The favoured plants all provided food and also cover in the case of *Phragmites* and *Urtica*. Shallow water was avoided even though its associated emergent macrophytes provided cover. Deep water may allow the water voles to escape predation by diving and swimming away.

Introduction

The water vole (*Arvicola terrestris* L.) has a wide Palaearctic distribution. In Europe it is often found away from water but the British populations are, with few exceptions, almost completely restricted to aquatic habitats (Boyce 1991).

Most previous investigations of the water vole's habitat have been conducted in Europe and have been largely qualitative emphasising the importance of food plants (Wijngaarden 1954; Zejda and Zapletal 1969; Gaisler and Zejda (1974). More recently, Lawton and Woodroffe (1991) conducted a quantitative survey of the habitat of water voles on rivers in the North Yorkshire moors where there were many gaps in their distribution. They found that areas inhabited by water voles were characterised by a high percentage of grass, steep bank angles and relatively high layering of the vegetation. Other sites containing apparently suitable habitat were unoccupied by water voles due to their isolation or mink *Mustela vison* predation.

This study used similar quantitative methods in an intensive investigation of the water vole's dispersion on a large, lowland river in Britain, where mink were absent, and attempted to identify the major biotic and abiotic variables correlated with the water voles' pattern of dispersion.

A nation-wide survey suggested a long-term decline of water vole populations in Britain this century, possibly associated with habitat changes and the spread of mink (Jefferies et al. 1989). Therefore it is important to identify the key features which determine the habitat preference of water voles.

The study area

The study was conducted at the Oxford University Field Station on the River Thames extending from the foot of Wytham Wood, near the entry of the Evenlode to the Thames, to the origin of Seacourt Stream (Fig. 1). The study concentrated on three fields with different forms of land use: Field A was

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5803-0160 $ 02.50/0

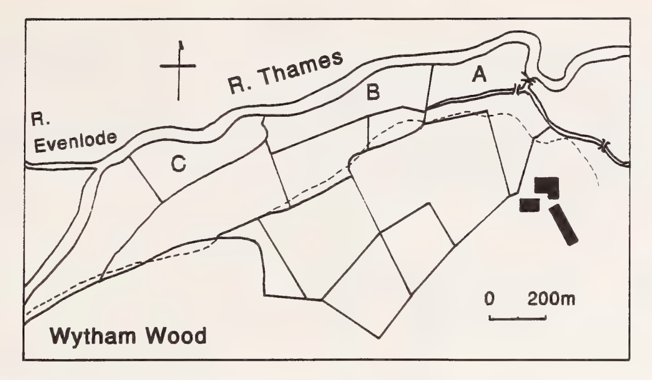


Fig. 1. The location of the three fields A, B, and C which formed the study area on the River Thames, north of Wytham Wood. The dashed line indicates the 61 m a. s. l. contour line

sown to grass in 1970 with several varieties of Perennial Rye grass and White Clover, and was used for silage and grazing; Field B was planted with Spring Barley each year; and Field C was an old permanent pasture used for grazing and hay-making. These forms of land use are fairly representative of the Upper Thames catchment (THAMES CONSERVANCY 1969) and have not changed greatly since the 18th century (GRAYSON and JONES 1955). The vegetation on the river bank is rather different from that found in the fields because, in addition to the riparian influence, it is never cut or harvested. However, it is grazed by cattle, with heaviest grazing in Field C and lightest in Field B which is only grazed for a very short period once the barley and straw have been harvested. The bank had a variety of plants, characterised by perennial dicotyledons (e.g. Stinging Nettle *Urtica dioica*, Creeping Thistle *Cirsium arvense* and Great Hairy Willow Herb *Epilobium hirsutum*) and emergent macrophytes (e.g. Soft Rush *Juncus effusus*, Bur-Reed *Sparganium erectum*, Common Reed *Phragmites communis*, Sweet Reedgrass *Glyceria maxima* and Reed Canary-grass *Phalaris arundinacea*).

Material and methods

Water vole numbers and distribution

Information on the distribution of water voles along the study area was obtained from a trapping programme. The study area was divided into 32 sections of river bank, each 50 m long. The number of individual water voles caught in each of these sections and the total number of water vole catches (including recaptures) was calculated for different periods within the year and for different age and sex groups. The three fields (A, B, and C) were not trapped with equal intensity because of the problems caused by the occasional presence of grazing cattle. Therefore the number of water vole catches in Fields A and C was corrected (× 1.45 and × 1.36 respectively) to reflect equal trapping intensity.

Water voles were caught in live traps made according to STODDART's (1970) design, with slight modifications, and were baited with apple. The traps were placed 20–25 m apart, so there were 2–3 traps in each section of the river bank, and every effort was made to place them in runways or other sites of water vole activity. At each monthly trapping session the position of individual traps was accurately located (to the nearest metre) by pacing between the traps to markers on the river bank (fences, trees, bushes, etc). Initial experiments showed that prebaiting was not necessary and traps were left in position for one day (February to November 1975) or two days (December 1975 to November 1976) each month. With slight variations in the numbers of traps available, and thus intertrap distances, traps were seldom placed in exactly the same position in successive trapping sessions.

In this discussion, a juvenile water vole refers to one born in the calendar year under discussion (i.e. an animal of the year) and an adult is a water vole which has survived at least one winter. Thus, at the end of December, all juveniles surviving to the following January become adults.

Physical features of the river bank

In June 1977, when water levels were near to normal, the bank profile was measured at 20 m intervals. A vertical, graduated pole was placed at the water's edge and the horizontal distance to the bank at 10 cm intervals up the pole was recorded. Similarly by floating a graduated plank attached to the

vertical pole, the depth of water at 10 cm intervals perpendicular to the bank was recorded. These measurements were plotted on graph paper and the following parameters obtained (Fig. 2): A: bank height; B: bank depth (distance from the vertical at maximum height; C: depth of water at 50 cm; D: depth of water at 100 cm; E: bank gradient (height/depth).

Surface soil samples, 10 cm deep, were taken at 20 m intervals on the river bank, 1 m from the water's edge. These were later hand textured and ranked from clay (5) to gravel (1). The aspect of the bank and the curvature of the bank (deviation from the mean direction of flow for 50 m upstream) were obtained from large-scale maps of the study area.

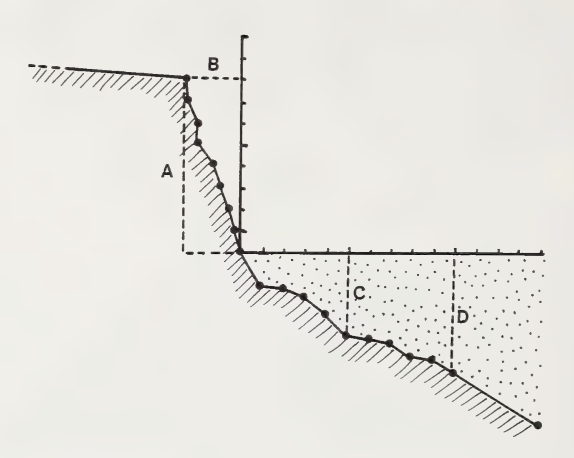


Fig. 2. Measurements taken from bank profiles in the study area: A = bank height; B = bank depth; C = water depth at 50 cm; D = water depth at 100 cm; E = bank gradient (A/B)

Vegetation

The vegetation parameters used in this analysis were obtained from a survey in August 1977 when most of the species (particularly the grasses) were still flowering and so could be readily identified. A quadrat extending 1 m from the water's edge and 0.2 m wide was located at 20 m intervals along the river bank (n = 78) and each species in the quadrat was given an importance value (1–10) based on 10 % intervals of its estimated percentage of coverage. Although this assessment of vegetation was relatively crude, it allowed a large number of sites to be sampled and provided some improvement on simple presence or absence data (Lambert and Dale 1964; Walker 1974).

Data analysis

To test whether the distribution of water vole captures in the study area was random or clumped, Morisita's Index of dispersion, I_δ was calculated. The significance of departures from random (1.00) was determined using tables in Southwood (1966).

To determine which environmental variables (or combinations of variables) best "explained" the distribution of the water vole on the study area (i.e. accounted for most of the variance from a mean value) various statistical methods were used. It must be emphasised that this type of analysis does not prove a cause and effect relationship for it is quite possible that a correlated variable is either merely spurious or is itself correlated with some other key variable. The results from these analyses must be used with biological reasoning.

First a correlation matrix was calculated to investigate the effects of individual variables on the water vole's dispersion. To investigate the effects of several variables, multivariate methods (multiple correlation, multiple regression, factor analysis) were then used. Two methods of factor analysis, Principal Component Analysis (PCA) and (Classical) Principal Factor Analysis (PFA) differing in their underlying models, were used. Since PCA, in particular, is very dependent on the variance of the original variables, it is important that these should be of the same order of magnitude, so all were standardised (mean = 0, variance = 1) as recommended by Harman (1976).

Results

The trapping programme produced two types of information: the distribution of individually marked animals, where the presence of an individual in a section is recorded only once; and the distribution of all catches, including recaptures. The former reduces the effect of repeated recaptures of "trap-happy" individuals but gives equal weighting to both an individual's core area and fringe areas, where it may be found only sporadically. The total number of catches clearly indicates sections where individuals are caught repeatedly. In practice both provided data which were strongly correlated (adult males: r = 0.81; adult females: r = 0.77; juveniles: r = 0.62) and the following analysis is restricted to the distribution of total catches (Fig. 3). In both cases, an underlying assumption is that the pattern of catches represents the pattern of activity and distribution – this is considered further in the discussion.

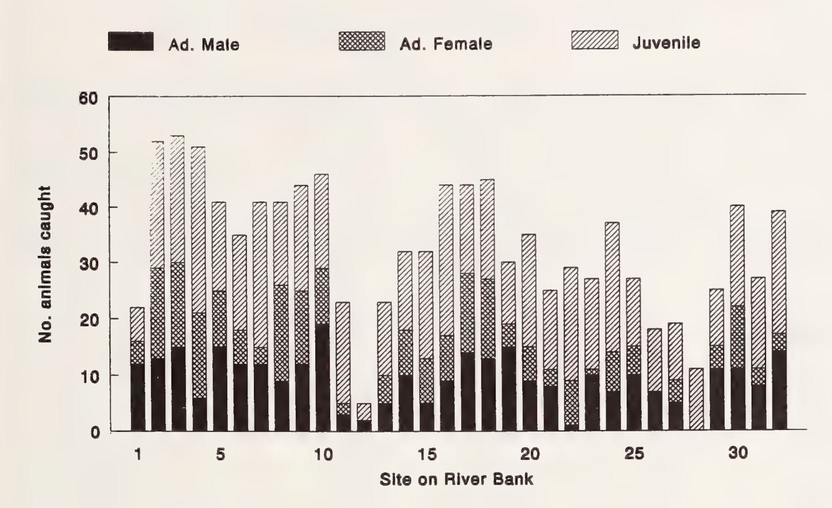


Fig. 3. The total numbers of adult male, adult female and juvenile water voles caught on the study area (corrected to equivalent trapping effort) in each 50 m section of the river bank

Dispersion of water voles

In the three fields under investigation, 815 catches of water voles were made in 2796 trap-nights. The distribution of these catches was clearly non-uniform (Fig. 3) and Morisita's index of dispersion (Tab. 1) showed significant clumping for all categories but least for adult males and most for adult females with juvenile males and females being intermediate. Other rodents were virtually absent in this habitat, a brown rat *Rattus norvegicus* was caught only once during the entire trapping programme. Stoats *Mustela erminea* and weasels *M. nivalis* were occasionally seen but never caught, and mink *M. vison* were never recorded in the study area.

The correlation of catches in the 32 positions between adult males and females was significant but low (r = 0.413, P < 0.05) and the catches of adult males were not significantly correlated with those of

Table 1. **Dispersion of water voles on the River Thames**

Water vole category	Morisita's Iδ
Total numbers	1.09*
Adult Males	1.12**
Adult Females	1.36**
Juvenile Males	1.28**
Juvenile Females	1.20**

Significance: * = $P < 0.05$; ** = $P < 0.01$.

juvenile males or juvenile females (r = 0.084, 0.190, P > 0.10 respectively). However, catches of adult females were significantly correlated with those of juvenile males and females (r = 0.402, 0.392, P < 0.05) and catches of juvenile males and juvenile females were strongly correlated with one another (r = 0.684, P < 0.001). In subsequent analyses juvenile males and females are lumped together.

Negative correlations were found between Morisita's Index of Dispersion and the estimated Mean Number Alive (Woodall 1978) when total water vole catches over five periods (Feb.–May 1975, June–Oct. 1975, Nov. 1975–Feb. 1976, Mar.–May 1976, June–Aug. 1976) were examined (r = 0.839, n = 5, 0.05 < P < 0.1). This may suggest that at higher population densities the water voles are more evenly dispersed but this result is complicated by seasonal factors and changes in the population structure with increasing proportions of juveniles at high densities.

Univariate analysis of habitat variables

Several variables reflecting physical dimensions of the environment showed significant correlations with water vole catches (Fig. 4, Tab. 2). Water depth at 100 cm from the bank was positively correlated with all categories of water voles, significantly so for total catches and adult females. Bank height was negatively correlated with catches of adult females and bank depth showed significant negative correlations with total catches and catches of adult males. Bank deviation showed a significant negative correlation with catches of adult females, this is difficult to explain but may reflect an association with some emergent plants (*Juncus effusus*, etc.).

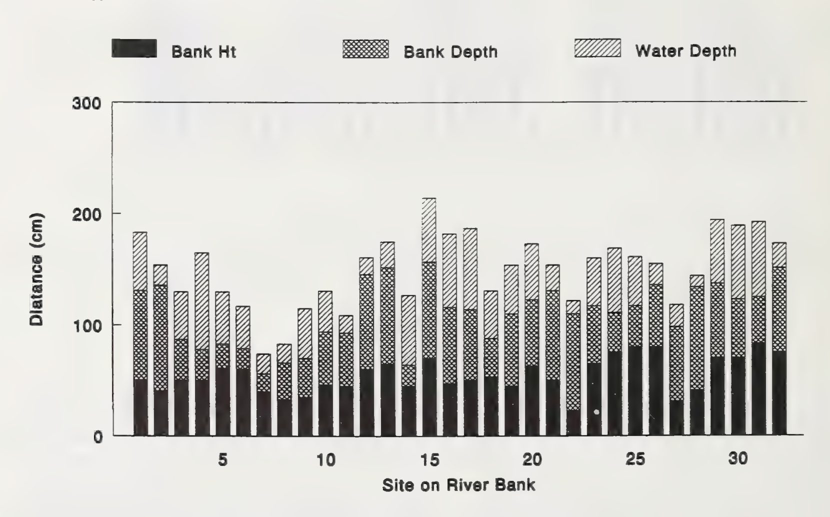


Fig. 4. Mean physical parameters (Bank height [A], Bank depth [B] and Water Depth at 100 cm [D]) at each section along the river bank

The vegetation on the river bank was quite diverse and, even after excluding 16 species which had total scores of < 10 (summed over the 32 positions), 18 species remained. One of these "species" consisted of grasses which had been grazed short to give a lawn-like appearance and which could not be identified to species. Hereafter it is referred to as Gramineae indet. The distribution of eight plants showed significant correlations with the distribution of water vole catches (Tab. 3, Figs. 5, 6). *Urtica dioica* and Gramineae indet. were positively correlated with total catches and those of adult males and females,

Table 2. **Correlations between the distribution of water voles and physical features of the river bank on the Thames**

River bank	Water vole			
	Total No.	Ad.Male	Ad.Female	Juv.
Bank height	−0.210	0.067	−0.340⁺	−0.164
Bank depth	−0.358*	−0.387*	−0.286	−0.132
Bank gradient	0.149	0.289	0.037	0.024
Depth at 50 cm	0.313⁺	0.288	0.188	0.220
Depth at 100 cm	0.429*	0.308⁺	0.349*	0.285
Soil texture	0.195	0.084	0.156	0.179
Aspect	0.023	0.049	0.207	−0.193
Deviation	−0.278	−0.028	−0.399*	−0.166

Significance: ⁺ = $0.1 > P > 0.05$; * = $P < 0.05$.

Table 3. **Correlations between the distribution of plant species and water voles on the River Thames**

Plant species	Water vole			
	Total No.	Ad.Male	Ad.Female	Juv.
Urtica dioica	0.505**	0.453**	0.417*	0.251
Polygonum amphibium	−0.295⁺	−0.369*	−0.130	−0.169
Rumex conglomeratus	−0.003	−0.041	0.271	−0.230
Erysimum cheiranthoides	0.116	0.209	0.184	−0.116
Filipendula ulmaria	−0.081	0.040	−0.105	−0.100
Epilobium hirsutum	0.137	0.074	0.006	0.213
Scrophularia auriculata	0.221	0.265	0.082	0.150
Cirsium arvense	−0.100	0.256	−0.051	−0.374*
Juncus effusus	−0.142	0.097	−0.316⁺	−0.072
Sparganium erectum	−0.302⁺	−0.203	−0.389*	−0.075
Glyceria maxima	0.097	−0.145	0.212	0.199
Dactylis glomerata	−0.042	0.049	−0.021	−0.109
Arrhenatherum elatius	−0.182	0.033	−0.259	−0.154
Holcus lanatus	−0.180	−0.114	−0.248	−0.035
Phalaris arundinacea	−0.336⁺	−0.381*	−0.271	−0.107
Phelum pratense	−0.197	−0.279	−0.158	−0.016
Phragmites communis	0.459**	0.249	0.299⁺	0.445**
Gramineae indet.	0.362*	0.372*	0.551**	−0.102

Significance: ⁺ = $0.1 > P > 0.05$; * = $P < 0.05$; ** = $P < 0.01$.

Phragmites communis was positively correlated with total catches and those of adult females and juveniles (Fig. 5).

Polygonum amphibium and *Phalaris arundinacea* were negatively correlated with total catches and those of adult males. *Sparganium erectum* was negatively correlated with total catches and those of adult females, *Juncus effusus* was negatively correlated with adult female catches and *Cirsium arvense* was negatively correlated with juvenile catches (Fig. 6).

Multivariate analysis of habitat variables

Multivariate analysis was used to investigate and display some of the interactions between variables. In view of the crude nature of some of the variables, this is used not as a rigorous statistical analysis but rather as an investigative tool.

The proportion of variance in the distribution of water vole catches "explained" by the

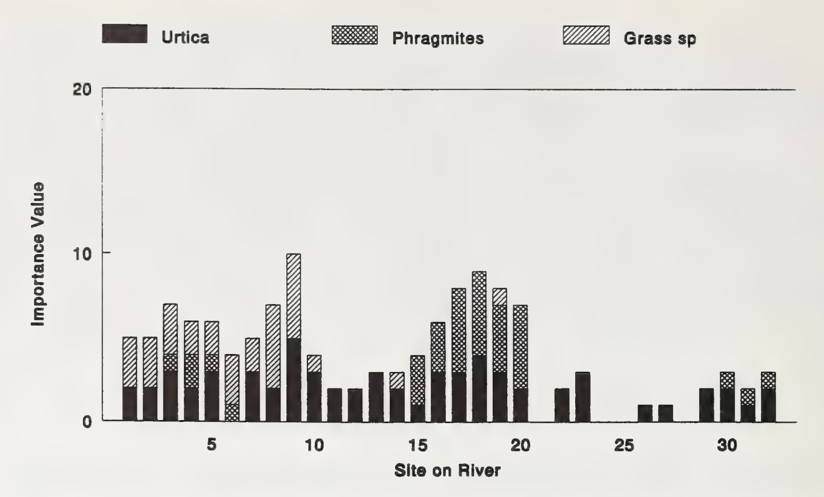


Fig. 5. Mean importance values (see text) at each section along the river bank for some plant species (*Urtica dioica, Phragmites communis*, Grass spp.) which showed significant positive correlations with water vole catches

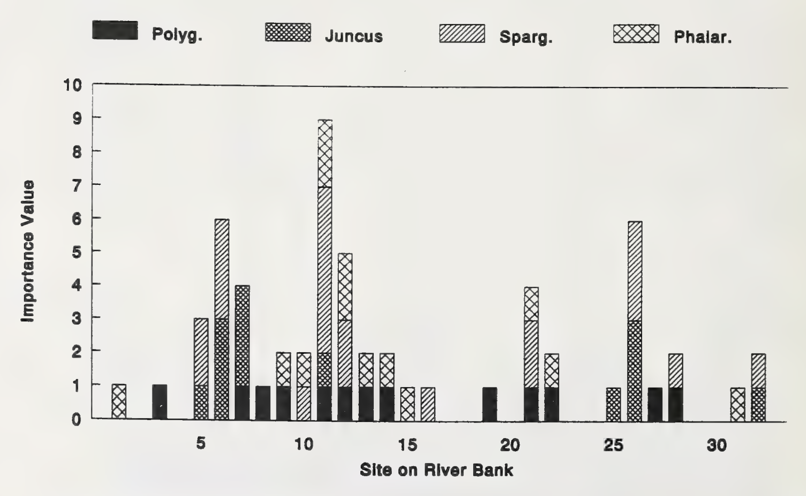


Fig. 6. Mean importance values (see text) at each section along the river bank for some plant species (*Polygonum amphibium, Juncus effusus, Sparganium erectum, Phalaris arundinacea*) which showed significant negative associations with water vole catches

12 environmental variables with significant univariate correlations was indicated by the square of the multiple correlation co-efficient (R^2): 0.55 for adult males; 0.79 for adult females and 0.64 for juveniles. These results correspond with the results of Morisita's index of dispersion showing adult females have the most clumped dispersion (thus more readily explained by environmental variables) while adult males have the least clumped dispersion and so are less explicable by the environmental variables.

Since many of the environmental variables were strongly correlated with one another, stepwise multiple regression did not extract many of the variables shown to be significant by univariate analysis, so Principal Component Analysis was used to reduce the variables to one or more factors which were orthogonal (i.e. uncorrelated).

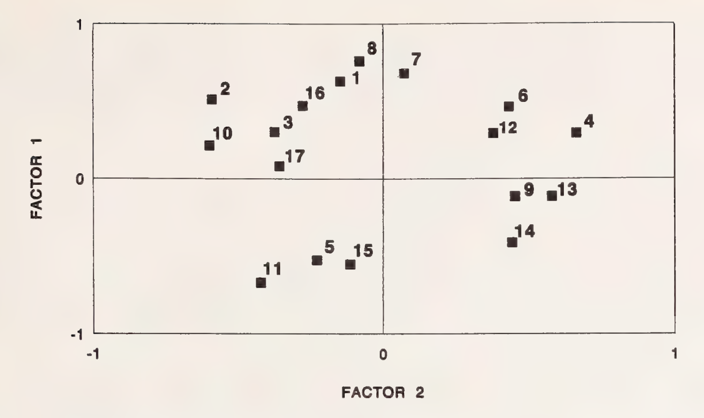


Fig. 7. The relative association of water vole numbers and vegetation and physical parameters on two factors generated by Principal Factor Analysis. 1 = adult male water voles; 2 = adult female water voles; 3 = juvenile water voles; 4 = bank height; 5 = bank depth; 6 = bank gradient; 7 = water depth at 50 cm; 8 = water depth at 100 cm; 9 = deviation of river bank; 10 = *Urtica dioica*; 11 = *Polygonum amphibium*; 12 = *Cirsium arvense*; 13 = *Juncus effusus*; 14 = *Sparganium erectum*; 15 = *Phalaris arundinacea*; 16 = *Phragmites communis*; 17 = Gramineae indet

Including only those variables with significant correlations with water vole numbers, both PCA und PFA (with varimax rotation and 1 factor fixed) gave similar results (Fig. 7). Water vole numbers, especially adult males and females, had high positive loadings on Factor 1 together with water depth at 50 and 100 cm, and *Phragmites communis*. Variables with strong negative loadings on Factor 1 included Bank Depth, *Polygonum, Sparganium* and *Phalaris*. This factor seems to represent a trend from deep water and associated *Phragmites communis* to a large bank depth, shallow water and its associated plants.

Female water voles, and to a lesser extent juveniles, had high negative loadings on Factor 2, together with *Urtica* and short Gramineae indet. Bank height, bank gradient, deviation, *Cirsium*, and *Juncus* had high positive loadings on Factor 2. This factor seems to represent a trend from high banks, and steep gradients to lower banks with *Urtica* and short Gramineae indet.

Discussion

This study assumes that, with equal trapping effort, the varying number of water voles caught in different parts of the study area reflected varying intensities of utilization of the area by water voles. Trapping is not the best method of investigating an animal's spatial activities, since it interrupts the activity and may preferentially sample certain portions of the population. However, other methods of recording activity also have drawbacks and without using radio telemetry (which usually limits sample size), trapping seems to be a practical if not ideal alternative (Grant and Morris 1971). Other measures of water vole activity (holes in the river bank, latrines, food remains) were all associated with areas where water voles were caught frequently and areas where water voles were seldom caught lacked these signs of their activity. Therefore, the trapping results seem to have provided a useful measure of the water vole's dispersion patterns and activity.

Dispersion

The dispersion of water voles in the study area was clumped, significantly different from a random pattern. There was some indication that their dispersion became more random and

less clumped as the population density increased and similar results were found by Grant and Morris (1971) for *Microtus pennsylvanicus*. However, this result is confounded by the fact that at high densities much of the population was made up of juveniles that may show less clumping than adults. Sample sizes were inadequate to analyse adults alone at different seasons.

These results differ from those of Stoddart (1970) who found that water voles were evenly distributed along a stream in Scotland with no indication of clumping. This was probably due to a much more uniform habitat. They also differ from Lawton and Woodroffe's (1991) study in the North Yorkshire Moors National Park where they found major gaps in the distribution of water voles along the rivers, explained by unsuitable habitat, mink predation and isolation. In this study on the Thames no section was completely avoided (Fig. 3) although some areas were much more heavily used than others. The possible reasons for this are considered below.

Adult males showed less habitat selectivity than females: their dispersion was less clumped and less of the variance of their capture sites could be accounted for by the environmental variables. This is consistent with the significantly larger home ranges of males (Stoddart 1970; Boyce 1991) particularly in summer (Woodall 1978) which means that they move over a wider range of habitats than do the females.

Correlations between the capture locations of juvenile males and females were very high, as were the correlations between juveniles and adult females. This is not unexpected since young juveniles can be expected to remain in their natal area for some time before dispersing. Correlations between capture sites of adult males and juveniles were much lower.

Environmental correlates

Several environmental variables showed significant correlations with the pattern of water vole catches. Multivariate methods showed that between 55 % (adult male) and 79 % (adult female) of the variance of captures could be accounted for by these variables. This is a similar or higher level than that reported for *Microtus pennsylvanicus* (Grant and Morris 1971).

Environmental variables correlated positively with water vole captures included water depth at 100 cm, and the presence of *Urtica dioica*, *Phragmites communis* and Gramineae indet. while negative variables were largely those associated with shallow water (large bank depth, *Polygonum amphibium*, *Sparganium erectum*, and *Phalaris arundinacea*).

Vegetation may provide food or cover or both, and different methods of measuring the vegetation will focus on these different aspects. A physiognomic approach will provide structural information emphasizing the importance of cover while a floristic approach gives information on the relative abundance of dietary species and their contribution to cover must be inferred from knowledge of their growth form. The latter approach was used here.

Plant species positively associated with water voles were all important food items. Holisova (1970) examined stomach contents of water voles trapped on the edge of a shallow lake and found that *Phragmites communis* was the most frequently consumed species, clearly preferred over other emergent macrophytes, *Typha* spp. Boyce (1991) also records *Phragmites* as an important food item and this was supported by observations on the study area. *Urtica* has also been regularly recorded as an important food item for water voles (Holisova 1965; Ashby and Vincent 1976; Woodall 1978).

The category "Gramineae indet." referred to areas where the grass had been grazed short ("lawns") and, lacking flowers or extensive leaves, could not be identified to species. Such areas were significantly correlated with captures of adult females in particular, and are recognised as distinctive signs of water voles' presence (Stoddart 1977). The negative correlation between *Cirsium arvense* and juvenile water vole captures may reflect avoidance of the plants' protective spines by the juveniles.

Many of the environmental variables may be important in allowing water voles to evade predators. This study provided no direct evidence on the type or level of predation experienced by this population although several animals were caught with part of their tails bitten off, but in the literature there are many reports of the wide variety of mammals, birds and even fish that will attack water voles (SOUTHERN 1964; HOWES 1979; BOYCE 1991).

Smaller rodents are able to reduce predation either by being nocturnal or by remaining under cover while active. BIRNEY et al. (1976) have shown the importance of cover to *Microtus* populations, especially when at high density. The large size of the water vole (up to 10 × the mass of *Microtus*) may preclude it from using vegetation as cover except in those localities, such as rivers, where the vegetation grows very dense and remains so for most of the year. LAWTON and WOODROFFE (1991) found that relatively high layering of the vegetation was associated with core areas and suggested that this might allow water voles to remain hidden from predators while foraging out of the water. Some of the plants identified as positively correlated with water vole catches in this study (*Phragmites* and *Urtica*) grew in dense clumps and so provided both food and cover. HOWES (1979) gives three instances of where the removal of waterside vegetation led to a higher frequency of water vole remains in fox scats or barn owl pellets.

An important alternative escape mechanism of the water vole is to dive off the bank and then to swim away, entering an underwater tunnel or emerging some distance away (ZEJDA and ZAPLETAL 1969; STODDART 1977; pers. obs.). This is clearly facilitated by deep water because if the water vole dives into shallow water it may still be caught by the predator (e.g. a heron). Water depth at 100 cm from the bank had the highest correlation with water vole catches of any abiotic variable considered in this study indicating the importance of this feature. In Sweden, water voles are more terrestrial and also constitute a much higher proportion of weasels' diet (ERLINGE 1975) than they do in Britain (KING 1991).

Even the cover provided by dense clumps of emergent *Sparganium, Phalaris* and *Juncus* in sections 5, 6, 7, 11 and 12 were little frequented by water voles. Although these plants are all eaten by water voles (HOLISOVA 1965, 1970; WOODALL 1978; HOWES 1979), they are not preferred species (pers. obs.) and their association with shallow water probably made the sections unattractive to the voles.

LAWTON and WOODROFFE (1991) noted the importance of steep bank angles but did not specifically measure water depth and K. R. ASHBY (pers. comm. in BOYCE 1991) has remarked on the importance of deep water. High banks and steep bank gradients were not favoured by water voles in this area possibly because in some sections erosion and collapse of the banks led to shallow water off-shore.

The variables identified as important in this study have also been recognised in earlier more qualitative studies. ZEJDA and ZAPLETAL (1969) obtained similar results from a study of water voles in Central Moravia where they reported that a high bank, covered with "grass, ruderal or littoral vegetation" but not wooded, and deep water were all favourable to water voles. GAISLER and ZEJDA (1974) in a study of water voles on a pond, obtained their highest catches from trap stations "near slopy banks, covered with grass stands and neighbouring with fields and, at the same time, with luxuriant vegetation at the water's edge".

The variables that characterised the core sites in LAWTON and WOODROFFE's (1991) study (a high percentage of grass, steep bank angles, and relatively high layering of the vegetation) were similar to those identified as important in this study, although the need to consider water depth in addition to bank heights and gradients was identified. The similarity in these results from studies conducted in different locations, on different sizes of rivers and with differing levels of predation gives some assurance that the key factors determining water vole distribution have been identified.

Acknowledgements

I am most grateful to my wife, Leith, and to members of the Animal Ecology Research Group, especially my supervisor Dr M. J. Coe, for much assistance; to the Department of Zoology for providing facilities for this project; to the Department of Agriculture for allowing me to work on the University Farm and to the Rhodes Trustees for financial support. Prof. D. M. Stoddart kindly provided comments on a draft of this paper.

Zusammenfassung

Verteilung und Habitatwahl der Schermaus (Arvicola terrestris) an der Themse

An einem 1,6 km langen Uferabschnitt der Themse bei Oxford, England, wurde die Verteilung von Schermäusen zwei Jahre lang untersucht. Die Tiere traten stellenweise gehäuft auf; dies galt am deutlichsten für adulte Weibchen, weniger für Jungtiere und am wenigsten für adulte Männchen. Das Flußufer wurde in 32 Abschnitte von 50 m Länge eingeteilt. Daten über die Vegetation und Geomorphologie der Abschnitte wurden mit den Häufigkeiten von Schermausfängen in Beziehung gesetzt. Diese Analyse ergab, daß die Schermausfänge positiv korrelierten mit der Wassertiefe, mit dem Vorkommen von *Urtica, Phragmites* und Gräsern, und negativ mit der Uferhöhe, Uferbreite, *Polygonum, Phalaris, Spargianum* und *Juncus*. Alle bevorzugten Pflanzen dienen als Futter und bieten im Falle von *Phragmites* und *Urtica* auch Deckung. Flachwasser wurde gemieden, selbst wenn vorhandene Makrophyten Deckung boten. Tiefes Wasser erlaubt den Schermäusen vermutlich, möglichen Prädatoren durch Tauchen und Fortschwimmen zu entkommen.

References

Thames Conservancy (1969): Report of survey 1969. London: Thames Water Authority.
Ashby, K. R.; Vincent, M. A. (1976): Individual and population energy budgets of the water vole. Acta Theriol. **21**, 499–512.
Birney, E. C.; Grant, W. E.; Baird, D. D. (1976): Importance of vegetative cover to cycles of *Microtus* populations. Ecology **57**, 1043–1051.
Boyce, C. C. K. (1991): Water vole. In: The Handbook of British Mammals. Ed. by G. B. Corbet and S. Harris. 3rd Ed. Oxford: Blackwell Scientific Publs.
Erlinge, S. (1975): Feeding habits of the weasel *Mustela nivalis* in relation to prey abundance. Oikos **26**, 378–384.
Gaisler, J.; Zejda, J. (1974): Notes on a population of the water vole (*Arvicola terrestris* Linn.) on a pond. Zool. Listy **23**, 19–33.
Grant, P. R.; Morris, R. D. (1971): The distribution of *Microtus pennsylvanicus* within grassland habitat. Can. J. Zool. **49**, 1043–1952.
Graystone, A. A.; Jones, E. W. (1955): Notes on the history of Wytham Estate with special reference to the woodlands. Oxford: Holywell Press.
Harman, H. H. (1976): Modern Factor Analysis. 3rd ed. Chicago: University of Chicago Press.
Holisova, V. (1965): The food of the water vole, *Arvicola terrestris*, in the agrarian environment of South Moravia. Zool. Listy **14**, 209–218.
Holisova, V. (1970): Trophic requirements of the water vole, *Arvicola terrestris* Linn., on the edge of stagnant waters. Zool. Listy **19**, 221–233.
Howes, C. A. (1979): A review of the food and mortality of water voles in Yorkshire. Naturalist **104**, 71–74.
King, C. M. (1991): Weasel. In: The Handbook of British Mammals. Ed. by G. B. Corbet and S. Harris. 3rd Ed. Oxford: Blackwell Scientific Publs.
Lambert, J. A.; Dale, M. B. (1964): The use of statistics in phytosociology. Adv. Ecol. Res. **2**, 55–99.
Lawton, J. H.; Woodroffe, G. L. (1991): Habitat and the distribution of water voles: why are there gaps in a species range? J. Anim. Ecol. **60**, 79–91.
Southern, H. N. (1964): The handbook of British mammals. 1st Ed. Oxford: Blackwell Scientific Publs.
Southwood, T. R. E. (1966): Ecological Methods. London: Chapman and Hall.
Stoddart, D. M. (1970): Individual home range, dispersion and dispersal in a population of water voles (*Arvicola terrestris* [L.]). J. Anim. Ecol. **39**, 403–425.
Stoddart, D. M. (1977): Water vole. In: The Handbook of British Mammals. 2nd Ed. Ed. by G. Corbet and H. N. Southern. Oxford: Blackwell Scientific Publs.
Walker, B. H. (1974): Some problems arising from the preliminary manipulation of plant ecological data for subsequent numerical analysis. Jl. S. Afr. Bot. **40**, 1–13.
Wijngaarden, A. van (1954): Biologie en Betrijding van die Woel rat *Arvicola terrestris terrestris* (L.) in Nederland. Eindhoven.

Woodall, P. F. (1978): Aspects of the ecology and nutrition of the water vole *Arvicola terrestris* (L.). Unpub. D. Phil. thesis, Univ. Oxford.

Zejda, J.; Zapletal, M. (1969): Habitat requirements of the water vole (*Arvicola terrestris* Linn.) along water streams. Zool. Listy **18**, 225–238.

Author's address: Dr. Peter F. Woodall, Department of Anatomical Sciences, University of Queensland, Brisbane, Australia, 4072

Z. Säugetierkunde 58 (1993) 172–180

ISSN 0044-3468

Migrations of *Mus musculus musculus* in Danish farmland

By M. Carlsen

Zoological Museum of Copenhagen, Denmark

Receipt of Ms. 10. 7. 1992
Acceptance of Ms. 12. 10. 1992

Abstract

Examining the migrations of *Mus musculus musculus* to and from Danish farms trappings were carried out at two farms and the surrounding field boundaries every third to fourth week for one year. The mice were captured in barns, stables and farm houses from November to March. In April, while the populations of native rodent species were low, *M. m. musculus* emigrated to grass and herb covered parts of the field boundaries. From May to July few *M. m. musculus* were captured near buildings and in field boundaries, possibly because they spend the summer in cultivated fields. In early August they reappeared in the field boundaries. From August to November during a heavy increase of native rodent populations *M. m. musculus* immigrated from field boundaries to the immediate surroundings of the buildings and further into barns and stables and finally into farm houses.

The habitat choice of *Mus musculus musculus* was examined. The mice showed a preference for traps placed in grass and herb covered areas without trees or bushes. All *M. m. musculus* captured in tree and bush covered areas were transient.

Introduction

In the nothern part of Europe *Mus musculus* movement culminates in spring and autumn (Rowe et al. 1963; Vlcek 1984; Rowe et al. 1987). *M. m. musculus* is believed to migrate from human settlements to outdoor locations, eg. arable land, in spring and back again in autumn (Stein 1955; Jensen 1966; Reichstein 1978). These seasonal migrations seem to be uninvestigated.

Choice of outdoor habitat by *Mus musculus* in Northern Europe is insufficiently described. During investigations of the small mammal fauna in stands of trees and bushes, in hedges or in dunes *Mus musculus* is caught in very small numbers (Pollard and Relton 1970; Yalden 1980; Kozakiewicz 1987; Fairley and Smal 1987). Feral populations of *Mus musculus* on arable land have been found (Southern and Laurie 1957; Zejda 1975).

Information on habitat choice by feral populations of *Mus musculus musculus* in Denmark is non-existing.

The main purpose of this investigation is to describe, temporally and spatially, the seasonal migrations undertaken by *Mus musculus musculus* in farmland of south eastern Denmark. Furthermore the outdoor habitat choice of *M. m. musculus* during migration will be described.

Material and methods

162 Ugglan live-traps were set up at two slightly disrepaired farms in the southern part of Sjælland, Denmark. The farms are situated in low altitude farmland bordering on Dybsø and Avnø Fjords. The distance between the farms is about 6 km. None of the farms are closer than 2 km to forests. The field boundaries around the two farms consist of low banks/stone fences with a mixed growth of willows *Salix* sp., poplars *Populus* sp., elders *Sambucus* sp., rowan trees *Sorbus* sp., hawthorns *Crataegus* sp., blackthorns *Prunus spinosa*, dog roses *Rosa canina* and cherry plum trees *Prunus ceresifera*. Parts of the field boundaries, however, are without any trees or bushes (Figs. 1, 2).

The undergrowth mainly consists of grasses, stinging-nettles *Urtica* sp., thistles *Carduus* sp., bindweeds *Convolvulus/Calystegia* sp., mugworts *Artemisia* sp. and dewberry *Rubus caesius*. The

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5803-0172 $ 02.50/0

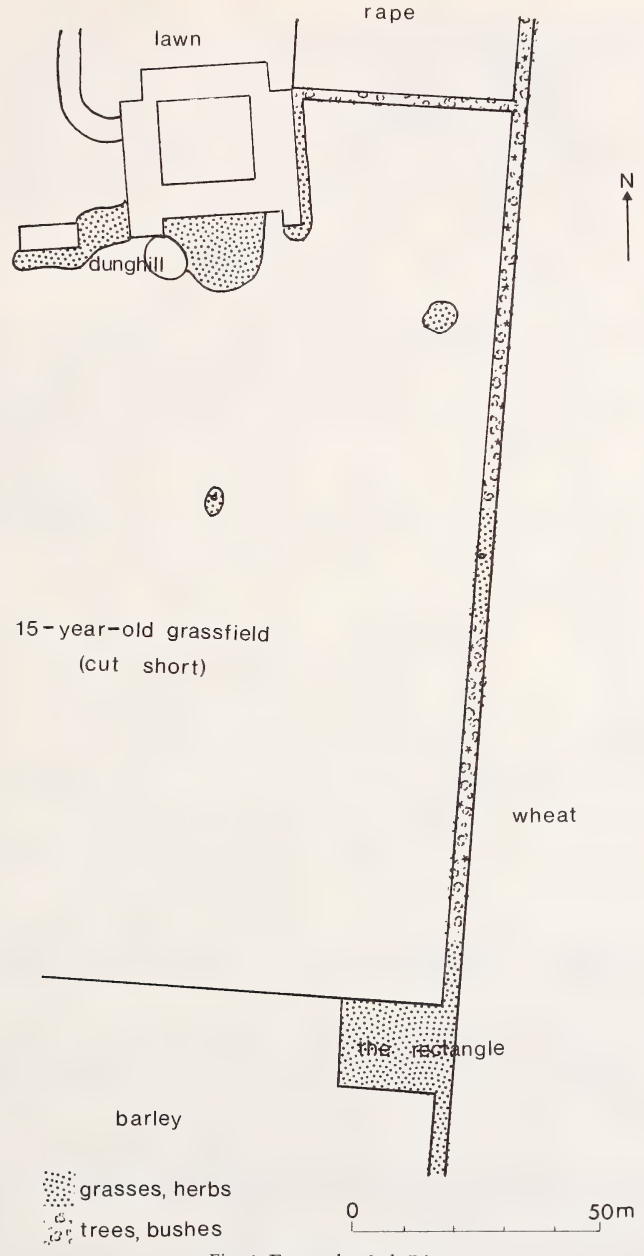


Fig. 1. Furmarksgård, Ring

cereal fields in the area were cropped from early July to early August and had all been ploughed by the end of August. The sugar beets were not cropped until late autumn.

Furmarksgård (Fig. 1) is situated in open farmland just west of the village Ring. In 1990 the stock consisted of 2 pigs, 8 to 12 bull-calfs, a dog and an unknown number of cats. During the winter 89/90 the farm was infested with rats *Rattus norvegicus*. On the request of the farmer the rats were eradicated during March 1990.

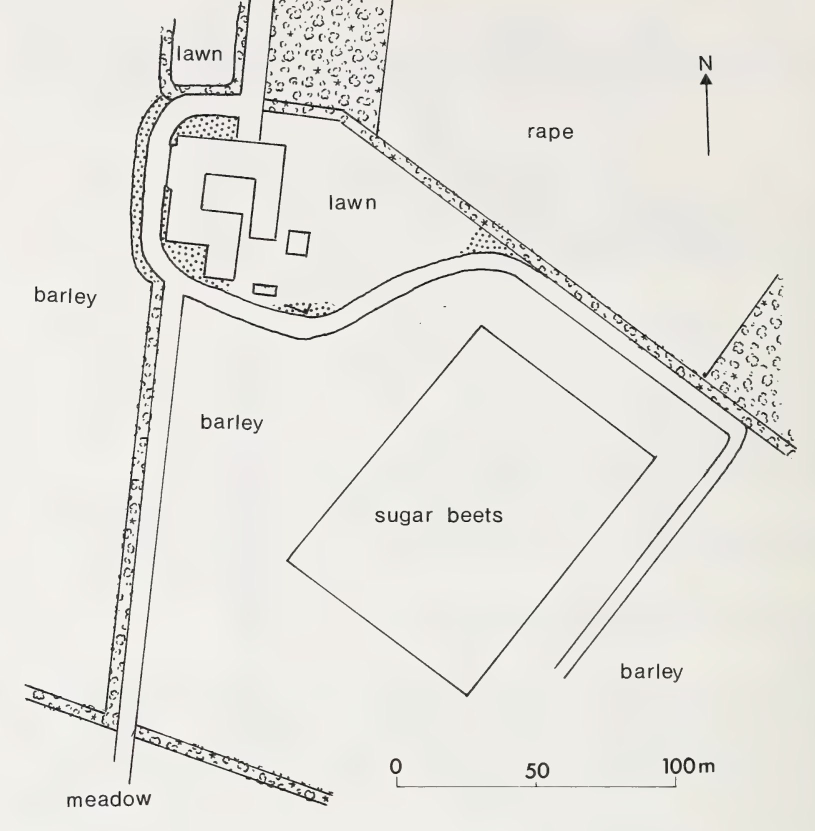


Fig. 2. Egebjerggård, Svinø

Barley and carrots were stored in the barn throughout the year. Filling of the loft with bundles of straw took place through the last half of July and into early August. From then on the amount of straw on the loft declined until it reached a minimum in June. Through June and the first half of July the loft was nearly empty.

92 Ugglan live-traps were set up on Furmarksgård: 18 in barn, stables and on the loft; 8 outdoors on the farm; 4 in the grass field; 9 in the east hedge (one every 5th meter); 1 on the 10th meter of the north hedge; 50 in the south hedge (one every 5th meter the first 250 meters) and 2 in the rectangle (Fig. 1). On a couple of occasions traps were extraordinarily set up from 250 to 500 meters in the south hedge.

Egebjerggård (Fig. 2) is in the southern end of the village Svinø. The only domestic animals on the farm were cats, 2 dogs, a few rabbits and poultry. In the stables piles of junk, such as bricks, boards and a few old bundles of straw could be found. The loft was empty. In the barn barley was stored in two silos from July 1990 and forward.

Around Egebjerggård 70 Ugglan live-traps were set up: 6 in barn and stables, 13 outdoors on the farm, 18 in the south east hedge (one every 5th meter from 0 to 80 meters and one on the 150th meter) and 33 in the south hedge (one every 5th meter). On a few occasions traps were set up from 150 to 450 meters in the south east hedge and in the farm-house.

As mentioned most traps were set up in the hedges with 5 meter intervals. Each trap was carefully placed where the chance of catch was judged to be the best. No individual trap was ever placed in the same spot during two consecutive trapping periods. This happened to eliminate as far as possible the possibility of the smell or functionality of the trap influencing the catch.

In periods of windy or rainy weather exposed traps were provided with plastic covers to keep water out.

The traps were baited with maize and coarsely rolled oatmeal. From late November 1989 to March 1990 traps were set up once a month. From April 1990 to early November 1990 traps were set up every 3rd week. However there was a 5-week-interval between the trapping period in the middle of May and the period in late June.

Trappings were carried out at both farms simultaneously. The traps were inspected once every 24 hours as early in the day as possible.

When a mouse was trapped it was individually marked by toeclipping. Species, mark, point of trapping, and if possible sex and weight were noted. The mouse was released at the point of capture immediately after the marking and weighing.

Results

3648 captures of 1154 individual small mammals distributed on 11 species were made on the two farms. The distribution on species and localities is shown in the Table.

The majority of *M. m. musculus* (98.4 %) were caught from late August to May with a peak (58.6 %) in September–November. Of 51 individuals marked in Svinø and 61 marked in Ring from November to October 27.5 % and 31.1 % respectively were caught in one trapping period only but on more than one day. 41.2 % and 29.5 % respectively were caught in more than one period. The sex ratio was close to 1:1 among all marked *M. m. musculus* as well as among the ones that were caught again.

Numbers of trapped individuals of small mammals

	Svinø	Ring
Sorex araneus	64	58
Sorex minutus	46	7
Neomys fodiens	5	–
Rattus norvegicus	1	–
Mus musculus	56	63
Apodemus sylvaticus	114	100
Apodemus flavicollis	60	85
Micromys minutus	39	96
Microtus agrestis	37	81
Clethrionomys glareolus	145	95
Mustela nivalis	1	1

During January and February *M. m. musculus* were only caught indoors. Through March and early April the majority of the mice were still caught indoors with only few individuals caught outdoors close to the farm buildings.

In the interval between the early April and late April trapping periods the mice in Ring moved from the loft to trap points in the rectangle 160 meters from the farm buildings (Fig. 1). This emigration was directly traceable. After the emigration no *M. m. musculus* were caught indoors but a few were still caught in hedges and near the buildings.

In Svinø all *M. m. musculus* captured indoors early April had disappeared by late April. An emigration could not be traced directly. The indoor mice in Svinø, however, disappeared simultaneously with the emigration in Ring. I therefore presume that the disappearance was caused by an emigration. The emigration coincided with a minimum in the populations of the other small rodent species of the area (Fig. 3).

In May 3 mice were caught in hedges, in June 1 indoors and in July 1 in a hedge.

In August *M. m. musculus* started appearing in growing numbers primarily close to the farm buildings. This immigration was most marked in Svinø. From the middle of September *M. m. musculus* were caught indoors as well, primarily in the barn and stables. From then on the percentage of the mice caught indoors increased while the outdoor percentage decreased (Fig. 4). In November 75 % of all *M. m. musculus* were caught indoors.

In Svinø the immigration was directly traceable. Several *M. m. musculus* could be traced from the south hedge to trap points near the farm buildings and farther into barn and stables and finally into the farm house (Fig. 5). A 16 g female was marked early August at a trap point in the south hedge 130 meters from the farm buildings. Late August it was

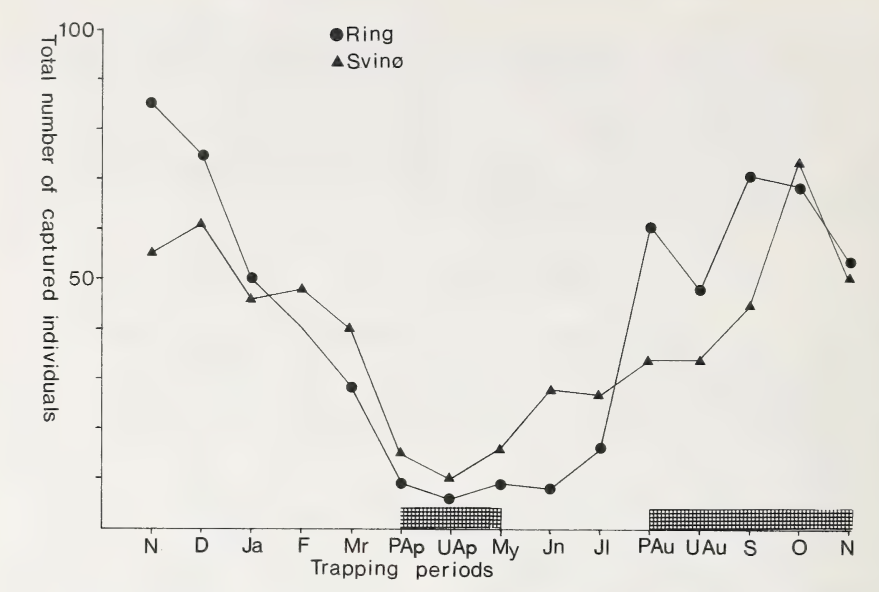


Fig. 3. Total number of captured individuals of 4 native rodent species (*C. glareolus, M. agrestis, A. flavicollis, A. sylvaticus*) each trapping period in Ring (dots) and Svinø (triangles). The shading shows the migration periods of *Mus musculus musculus*. N = November, D = December, Ja = January, F = February, Mr = March, PAp = Early April, UAp = Late April, My = May, Jn = June, Jl = July, PAu = Early August, UAu = Late August, S = September, O = October

caught close to the buildings and from September to November it was caught several times in the stables.

15 individuals were caught at more than one trap point. 13 of these had moved closer to the farm buildings or indoors between the catches.

In ring only few *M. m. musculus* were caught in the autumn of 1990. None were caught at more than one trap point.

The immigration took place from August to November, a wider span of time than the emigration. I presume that the immigration took place simoultaneously at the two farms as the mice in Ring reappeared near the farm buildings and later in the stables at the same times as in Svinø.

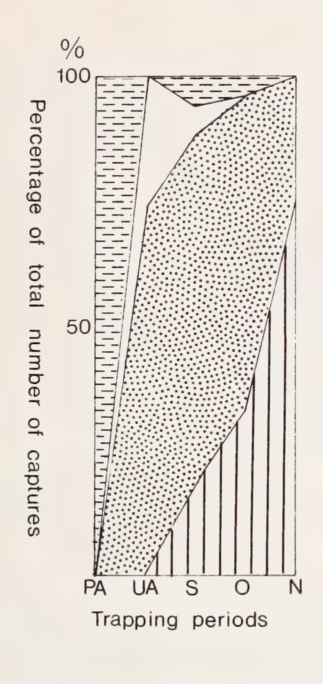
The immigration of *M. m. musculus* took place during a time of heavy increase in the populations of the other species of small rodents (Fig. 3).

The immigration was in 3 stages. The mice migrated from their summer quarters to the close vicinity of the farm buildings via the hedges or pherhaps directly from the fields bordering on the farm. After a short stay near the buildings the mice entered barn and stables. The farm house was entered either directly from the area immediately outside the buildings or via barn and stables.

The individual mice did not go through each particular stage simultaneously. In October, for instance, mice could be caught at all stages of immigration.

A female *M. m. musculus* marked on the loft in Ring in October emigrated in April. This indicates that individuals immigrating in autumn emigrate again in spring. None of the *M. m. musculus* which emigrated in spring returned in autumn.

Of 235 traps containing *M. m. musculus* 67.7 % held one individual and 32.3 % more than one (Fig. 6). 6 % of the traps contained 1–2 *M. m. musculus* with 1–2 individuals of other rodent species. The rodent species caught together with *M. m. musculus* were in 3 cases *Clethrionomys glareolus*, in 1 *Microtus agrestis*, in 3 *Apodemus sylvaticus*, in 1



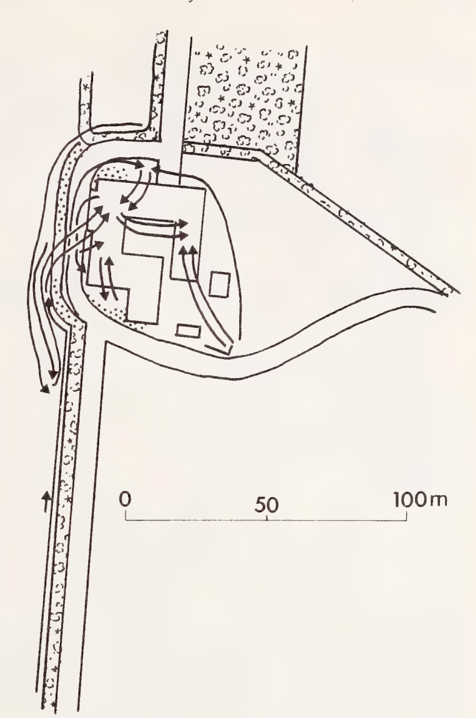


Fig. 4 (left). The immigration of *M. m. musculus*, Svinø, autumn 1990. Horizontal lines = Mice caught in hedges more than 75 m from the buildings. Blank = Hedges closer than 30 m to buildings. Dots = Immediately outside the buildings. Vertical lines = Indoors. PA = Early August, UA = Late August, S = September, O = October, N = November. – *Fig. 5 (right).* Movements of immigrating *Mus m. musculus*, Svinø, autumn 1990. Each arrow indicates the movements undertaken by one individual between two successive trap inspections

Apodemus flavicollis and in 6 cases *Micromys minutus*. In the 3 cases, however, where an *Apodemus sylvaticus* was caught together with a *M. m. musculus* these were the same two individuals.

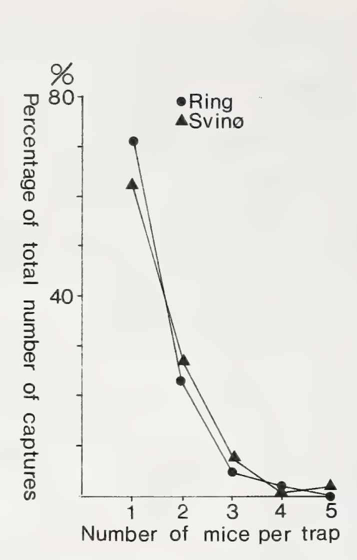
The individual trap point was rarely visited by more than one rodent species during a trapping period. From late August to November the individual outdoor trap points near the buildings visited by *M. m. musculus* were visited by a relatively steady number of mice. The total number of outdoor trap points visited by *M. m. musculus*, however, decreased. At the same time the number of trap points near the buildings visited by other small rodent species increased.

The outdoor trap points were classified as belonging to one of four categories of cover:

1. Close cover of grasses, nettles and other herbs; no trees or bushes (43 traps).
2. Piles of bricks, boards, broken concrete pipes etc. with vegetation of herbs and grasses; no trees or bushes (7 traps).
3. Trees or bushes with close undergrowth of grasses, nettles, etc. (73 traps).
4. Trees or bushes with sparse undergrowth (15 traps).

The number of catches at each category trap point were counted (Fig. 7).

The majority of *M. m. musculus* caught outdoors were caught in rather open habitats without trees or bushes. This in spite of the fact that the majority (63,8 %) of the traps were set under trees and bushes. All *M. m. musculus* caught more than once at a trap point were caught at points in categories 1 or 2.



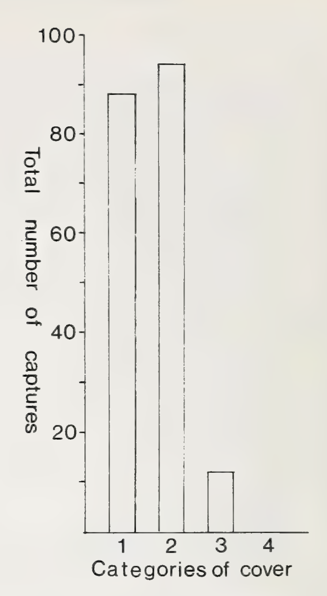


Fig. 6 (left). Captures of one or more *Mus m. musculus* per trap per trap inspection. – *Fig. 7 (right).* Outdoor habitat choice of *Mus m. musculus.* 1: cover of grasses and herbs; no trees or bushes; 2: piles of bricks, boards, etc. grass and herb cover; no trees/bushes; 3: trees/bushes; close undergrowth of grasses and herbs; 4: trees/bushes; sparse undergrowth

The 12 catches in category 3 are caused by 11 individuals. One individual only has been caught twice at category 3 trap points. The distance between the two involved trap points was more than 80 meters.

Discussion

Mus musculus are mainly caught in buildings and corn-ricks through autumn and winter (Rowe et al. 1963; Jensen 1966; Zejda 1975). Some populations spend the summer outdoors in the fields (Southern and Laurie 1974; Zejda 1975). Other populations spend all seasons indoors (Petrusewicz and Andrzejewski 1962; Pelikan 1974; Pelikan and Nesvadbova 1979; Vlcek 1984; Rowe et al. 1987).

Investigating the occurence of *M. m. domesticus* in arable land Southern and Laurie (1947) and Rowe et al. (1963) captured mice in hedges mainly in autumn but also in spring. Almost 3/4 of the mice leaving corn-ricks were noted in spring and almost 3/4 of the mice entering in autumn (Rowe et al. 1963).

In Czechoslovakia Vlcek (1984) found peaks in the intensity of *Mus musculus* movement in spring and autumn and Zejda (1975) could only catch *Mus musculus musculus* in fields from June to September and *M. m. spicilegus* from February to October.

All this indicates that yearly recurrent spring and autumn migrations between summer and winter quarters are undertaken by some *Mus musculus* populations in the northern half of Europe as suggested by Stein (1955), Jensen (1966) and Reichstein (1978).

This investigation clearly shows that populations of *Mus musculus musculus* in south eastern Denmark emigrate from human settlement in spring and immigrate in autumn. Hedges and field boundaries seem to be important migration routes.

Based on indoor trappings of *M. m. musculus* in Denmark Jensen (1966) suggests that immigration is not caused by human disturbance of the summer quarters of the mice in the fields as he does not find any surge in the immigration in connection with harvest or

ploughing of fields bordering on his house. ROWE et al. (1963), however, on the basis of trappings in corn-ricks and hedgerows found that the movements of *Mus musculus domesticus* living in the fields were largely influenced by farming practice.

Considering the multiple stages of the immigration an increase in numbers of immigrating *Mus musculus* caused by harvest or the like would not be noticed immediately in the buildings bordering on the fields but rather in the area just outside these buildings and in the hedgerows along the fields. By the time the mice reach the buildings the surge would be leveled by the intervening stages.

Mus musculus is a poor competitor with native rodent species (CALDWELL 1964; BERRY 1981; FAIRLEY and SMAL 1987) and interspecific competition might restrict it to disturbed areas uninhabited by native rodent species (DELONG 1966).

STEIN (1955) suggests that low feral *M. m. musculus* population numbers and retreat to buildings in autumn in eastern Germany could be caused by competition with *Apodemus sylvaticus*. Apparent competition between *Mus musculus* and *Apodemus sylvaticus* has also been found by BOITANI et al. (1985). The immigration of *M. m. musculus* in Svinø and Ring coincided with a heavy increase in native rodent populations, and it was mainly *Apodemus sylvaticus* which was responsible for the increase in trap points near the farm buildings in Svinø visited by other species than *M. musculus*.

I consider it possible that interspecific competition with other rodent species could be part of the cause for the immigration of *M. m. musculus*. When the summer habitat of *M. m. musculus* have been destroyed through harvest and ploughing the mice will probably be unable to find suitable uninhabited habitats away from human dwellings.

The wild forms of *Mus musculus* are typical dry area animals occuring in savannahs, steppes and even in desert country (SCHWARZ and SCHWARZ 1943). This investigation shows a preference by *M. m. musculus* when living outdoors for open habitats with dense cover of grasses, herbs, etc. but without cover of trees or bushes. This applies for spring as well as for autumn. Distribution and habitat choice of *Mus musculus* is influenced by competition more than by habitat structure (DUESER and PORTER 1986). With the habitat preference in spring and autumn being the same despite apparently different competitive pressures, however, I consider the shown preference reflecting the real preference well enough.

No resident *M. m. musculus* were ever captured in the tree and bush covered part of the field boundaries. Also no *M. m. musculus* were captured in the open grass and herb covered areas bordering on the outside of the farm buildings during the summer. However, the facts that the mice emigrated in small numbers in spring and immigrated in larger numbers in autumn show that outdoor breeding populations do exist during the summer.

In Europe *Mus musculus* have been found, sometimes abundantly, in cereal and root crops during the summer (SOUTHERN and LAURIE 1947; STEIN 1955; ZEJDA 1975; BOITANI et al. 1985). Information on the occurence of *Mus musculus* in open, undisturbed habitats in northern Europe seems to be scarce. Cultivated fields, meadows or other open habitats seem to suit the apparent habitat demands of *M. m. musculus*. Fields are in addition disturbed habitats with no or very low native rodent populations. This will minimize the chance of interspecific competition being a restricting factor for *M. m. musculus* populations.

I find it probable that *M. m. musculus* in south eastern Denmark spend the summer in cultivated fields.

Zusammenfassung

Saisonale Wanderungen der Hausmaus (Mus musculus musculus) im dänischen Ackerland

Um etwaige saisonale Wanderungen der Hausmaus (*Mus musculus musculus*) im dänischen Ackerland zu untersuchen, wurden auf zwei Höfen und in Flurbegrenzungen innerhalb eines Jahres jede dritte

oder vierte Woche Fallen aufgestellt. Von November bis März wurden die Mäuse in Scheunen, Ställen und Häusern gefangen. Im April, als die Populationen der wildlebenden Kleinnagetiere ein Minimum erreichten, wanderten die Mäuse zu den gras- und kräuterbewachsenen Teilen der Flurbegrenzungen. Von Mai bis Juli wurden nur wenige Hausmäuse in den Flurbegrenzungen und an Gebäuden gefangen, möglicherweise weil sie sich auf den Äckern aufhielten. Anfang August tauchten sie wieder in den Flurbegrenzungen auf. Von August bis November, als die Populationen der wildlebenden Kleinnagetiere ein Maximum erreichten, wanderten die Hausmäuse erst von den Flurbegrenzungen zu Regionen in unmittelbarer Nähe von Gebäuden, dann in Scheunen und Ställe und zuletzt auch in Häuser hinein.

Die Habitatpräferenz der Hausmaus wurde untersucht. Die Mäuse wurden vorwiegend in Fallen gefangen, die in gras- und kräuterbewachsenen baum- und buschlosen Gebieten aufgestellt waren. Alle *M. m. musculus*, die in baum- und buschbewachsenen Gebieten gefangen wurden, waren auf der Wanderung.

Acknowledgements

I would like to thank Hans Baagøe and Mogens Lund for valuable advice on the field sequence and comments, Mogens Andersen for advice, moral support and use of his office, Carl C. Kinze for help with the German Summary and finally the people of Egebjerggård and Furmarksgård who allowed me trapping mice on their property.

References

Berry, R. J. (1981): Biology of the House Mouse. Symposia zool. Soc. Lond. **47**, 395–425.

Boitani, L.; Loy, A.; Molinari, P. (1985): Temporal and spatial displacement of two sympatric rodents (*Apodemus sylvaticus* and *Mus musculus*) in a Mediterranean coastal habitat. Oikos **45**, 246–252.

Caldwell, L. D. (1964): An investigation of competition in natural populations of mice. J. Mammalogy **45**, 12–30.

DeLong, K. T. (1966): Population ecology of feral house mice: Interference by *Microtus*. Ecology **47**, 481–484.

Dueser, R. D.; Porter, J. H. (1986): Habitat use by insular small mammals: Relative effects of competition and habitat structure. Ecology **67**, 195–201.

Fairley, J. S.; Smal, C. M. (1987): Feral house mice in Ireland. Ir. Nat. J. **22**, 284–290.

Jensen, B. (1966): Musefangster indendørs. Flora og Fauna **72**, 130–136.

Kozakiewicz, A. (1987): Spatial distribution and interspecific interactions in small rodent community of a lake coastal zone. Acta Theriol. **32**, 433–447.

Pelikan, J. (1974): On the reproduction of *Mus musculus* L. in Czechoslovakia. Acta Sc. Nat. Brno **8**, 1–42.

Pelikan, J.; Nesvadbova, J. (1979): Small mammal communities in farms surrounding fields. Folia Zool. **28**, 209–217.

Petrusewicz, K.; Andrzejewski, R. (1962): Natural history of a free-living population of house mice (*Mus musculus* Linnaeus), with particular reference to groupings within the population. Ekol. Polska seria A **10**, 85–122.

Pollard, E.; Relton, J. (1970): Hedges V. A study of small mammals in hedges and cultivated fields. J. Appl. Ecol. **7**, 549–557.

Reichstein, H. (1978): *Mus musculus* Linnaeus 1758 – Hausmaus. In: Handbuch der Säugetiere Europas. 1. Ed. by J. Niethammer and F. Krapp, Wiesbaden: Akademische Verlagsgesellschaft.

Rowe, F. P.; Quy, J.; Swinney, T. (1987): Recolonization of the buildings on a farm by house mice. Acta Theriol. **32**, 3–19.

Rowe, F. P.; Taylor, E. J.; Chudley, A. H. G. (1963): The numbers and movements of house mice (*Mus musculus* L.) in the vicinity of four corn-ricks. J. Anim. Ecol. **32**, 87–97.

Schwarz, E.; Schwarz, H. K. (1943): The wild and commensal stocks of the house mouse, *Mus musculus* Linnaeus. J. Mammalogy **24**, 59–72.

Southern, H. N.; Laurie, E. M. O. (1947): The house mouse *Mus musculus* in corn-ricks. J. Anim. Ecol. **16**, 134–149.

Stein, G. V. (1955): Die Kleinsäuger ostdeutscher Ackerflächen. Z. Säugetierkunde **20**, 89–113.

Vlcek, M. (1984): Spacial activity of small mammals (*Rodentia*) in areas of large-scale livestock production farms. Vest. cs. Spolec. zool. **48**, 69–80.

Yalden, D. W. (1980): Urban small mammals. J. Zool. (London) **191**, 403–406.

Zejda, J. (1975): Habitat selection in two feral house mouse (*Mus musculus* L.) lowland populations. Zool. Listy **24**, 99–111.

Author's address: Michael Carlsen, Zoological Museum of Copenhagen, Universitetsparken 15, DK-2100 København Ø, Denmark

Z. Säugetierkunde 58 (1993) 181–190
© 1993 Verlag Paul Parey, Hamburg und Berlin
ISSN 0044-3468

A new subspecies of *Proechimys iheringi* Thomas (Rodentia: Echimyidae) from the state of Rio de Janeiro, Brazil

By Leila Maria Pessôa and S. F. dos Reis

Departamento de Zoologia, Universidade Federal do Rio de Janeiro and Departamento de Parasitologia, Universidade Estadual de Campinas, Brazil

Receipt of Ms. 26. 5. 1992
Acceptance of Ms. 3. 9. 1992

Abstract

Described a new subspecies of *Proechimys iheringi* based on specimens collected in the coastal sand plains of the state of Rio de Janeiro, southeastern Brazil. This new subspecies can be distinguished by a combination of traits that include an absence of cinnamon ground color in the subapical zone of setiform hairs, tail longer than head and body with a whitish brush in the tip, bullae large and well inflated, and by the structure of the septum of the incisive foramen, where the vomer is visible ventrally between the premaxillae and maxillae.

Introduction

Proechimys iheringi was originally described by Thomas (1911) on the basis of specimens from the Island of São Sebastião, off the coast of the State of São Paulo in southeastern Brazil. Later in 1948, Moojen reviewed the systematics of the Brazilian forms of the genus *Proechimys* and, in particular, greatly expanded the known distribution of *P. iheringi.* The population samples of *P. iheringi* that he examined ranged in distribution from the State of Bahia to the State of São Paulo; an area spanning approximately 2000 km. Moojen (1948) analysed variation in craniodental and pelage characters in this sample and described six subspecies in *P. iheringi*, viz. (Fig. 1): *P. i. denigratus* from Itabuna, State of Bahia; *P. i. panema* from Campinho, *P. i. paratus* from Capela de São Braz, and *P. i. gratiosus* from Floresta da Caixa D'agua, all in the State of Espírito Santo; *P. i. bonafidei* from Teresópolis, State of Rio de Janeiro; and *P. i. iheringi* from Island of São Sebastião, State of São Paulo.

Since the publication of Moojen's (1948) monograph the taxonomy of *P. iheringi* has not been reviewed. We have recently started, detailed studies of the taxonomy, systematics, and evolution of the taxa allocated to *P. iheringi* (Pessôa 1989, 1992; Pessôa and Reis 1991; Reis et al. 1992), and during the course of our work, have examined specimens collected in the coastal plains of the State of Rio de Janeiro that can be assigned to *P. iheringi* on the basis of dental, cranial, and pelage traits. These specimens, however, cannot be allocated to any of the previously recognized subspecies of *P. iheringi*, and are thought to represent a new subspecies described herein.

Material and methods

The identification of subspecies of *P. iheringi* was confirmed by comparison with types deposited in the Museu Nacional (Rio de Janeiro) and with the aid of diagnoses provided by Moojen (1948). Descriptions of hair characteristics are based on Moojen (1948), and hair measurements were taken (in mm) with an eyepiece micrometer. Capitalized color definitions follow Ridgway (1912). Seventeen cranial measurements (Tab. 1) were obtained with digital calipers accurate to 0.01 mm.

The specimens examined in this study are housed in the Museu Nacional (MN) and Museu de

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5803-0181 $ 02.50/0

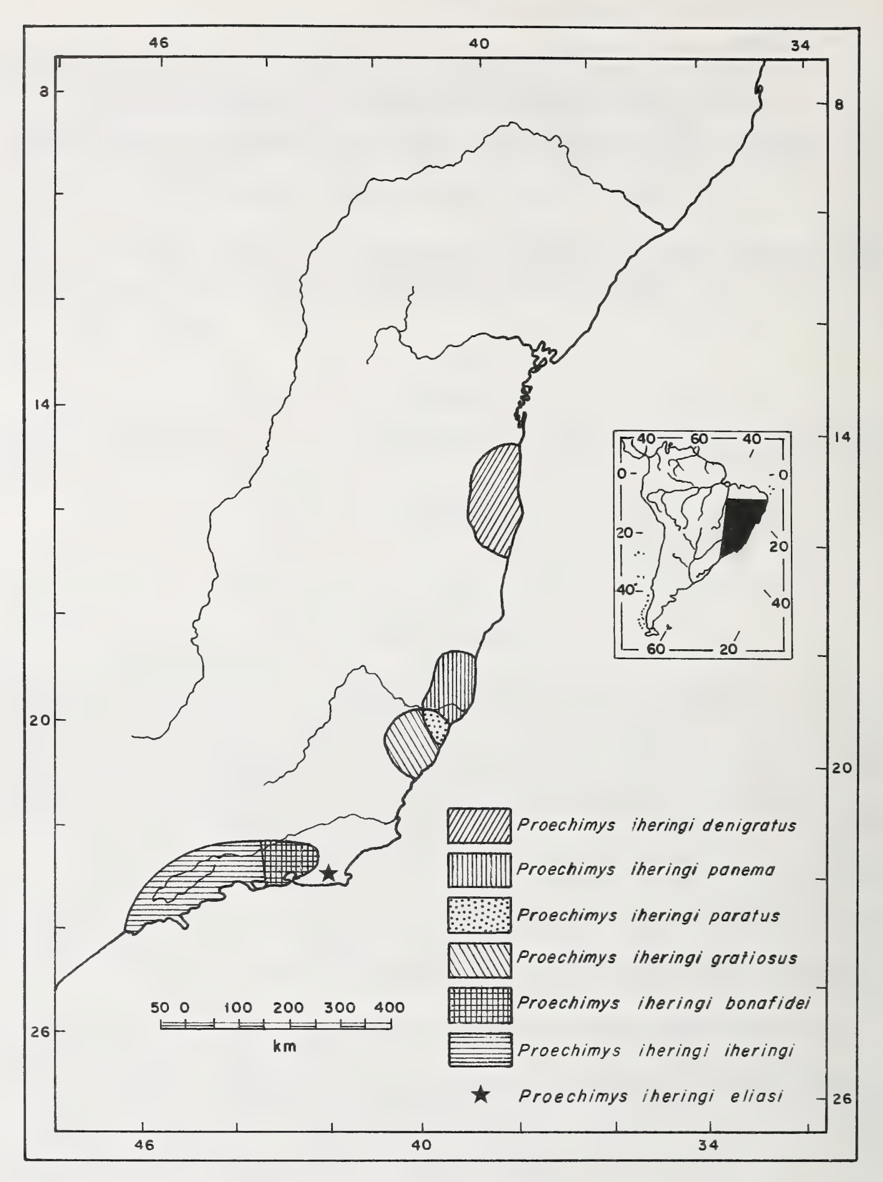


Fig. 1. Ranges for the subspecies of *Proechimys iheringi* according to Moojen (1948). The star denotes the type locality of *Proechimys iheringi eliasi*

Zoologia da Universidade de São Paulo (MZUSP). The following population samples were examined (Fig. 1): *P. i. denigratus* (Itabuna, State of Bahia [n = 8], MN 10474, 10476, 10477, 10515, 10517, 10519, 10521, 10528), *P. i. panema* (Campinho, State of Espírito Santo [n = 5], MN 8284–8288); *P. i. paratus* (Capela de São Braz, State of Espírito Santo [n = 4], MN 4012, 4023, 5455, 5458); *P. i. gratiosus* (Santa Teresa, State of Espírito Santo [n = 12], MN 4010, 4018, 4024, 4055, 5430, 5468, 5656, 5674, 5757, 5759, 5767, 5772); *P. i. bonafidei* (Teresópolis, State of Rio de Janeiro [n = 10], MN 6179, 6181–6183, 6187, 6780, 6782, 6784, 6786, 6787); *P. i. iheringi* (Island of São Sebastião, State of São Paulo [n = 6], MZUSP 218, 221, 222, 2095, 2145, 2146).

Results

Proechimys iheringi eliasi, new subspecies

Holotype: An adult male (MN 30524), dry skin, skull, and postcranial skeleton. Collected by L. M. Pessôa, J. A. de Oliveira and S. F. dos Reis on 28 July 1991 at Restinga da Barra de Maricá, Maricá, Rio de Janeiro, Brazil.
Type locality: Restinga da Barra de Maricá (22° 31′ S, 47° 17′ W), Município de Maricá, Rio de Janeiro, Brazil.
Other specimens: Eight specimens, all from Maricá (MN 26811, 26826, 26827, 26859, 28806, 28815, 28932, 30523).
Distribution: Known only from the type locality.
Diagnosis: The following combination of characteristics sets *Proechimys iheringi eliasi* apart from any other subspecies of *P. iheringi*: aristiforms wide and stiff, general color of upper parts blackish due to the lack of cinnamon ground color from subapical zone of setiforms; tail with whitish brush; bullae large and well inflated, nasals long; septum of incisive foramen complete and formed almost exclusively by premaxillae; maxillary portion of the septum short, vomer visible ventrally between premaxillary and maxillary portions of the septum.

Description

Pelage: General color on upper parts blackish and underparts white (Fig. 2). Aristiforms on middorsal region: gray basally, gradually blackening toward tip; total length (mean = 21.2 mm); maximum width (mean = 1.1). Aristiforms on outer thighs: gray basally, blackening distally with Ochraceous-Tawny tip; total length (mean = 17.6); maximum



Fig. 2. Type specimen of *Proechimys iheringi eliasi* (MN 30524), photographed alive

width (mean = 0.7). Setiforms on middorsal region: gray basally, gradually blackening toward tip; total length (mean = 15.7); maximum width (mean = 0.1). Setiforms on outer thighs gray basally, gradually blackening toward tip, but interrupted by a Cinnamon-Buff subapical zone; total length (mean = 14.0); maximum width (mean = 0.1).

Skull: Slender, nasals long, bullae large and well-inflated; jugals dorsoventrally wide with transverse ridge conspicuous; post-orbital process of zygoma conspicuous, formed almost exclusively by jugal; mesopterygoid fossa extending forward as far as the posterior plane of second molars; posterior palatine foramina at anterior plane of first molars (Fig. 3); incisive foramen elongate and narrow; vomerine septum complete and formed almost exclusively by premaxillae; maxillary part of vomerine sheath short; vomer visible ventrally, included between the premaxillary and maxillary portions of the vomerine septum (Fig. 4).

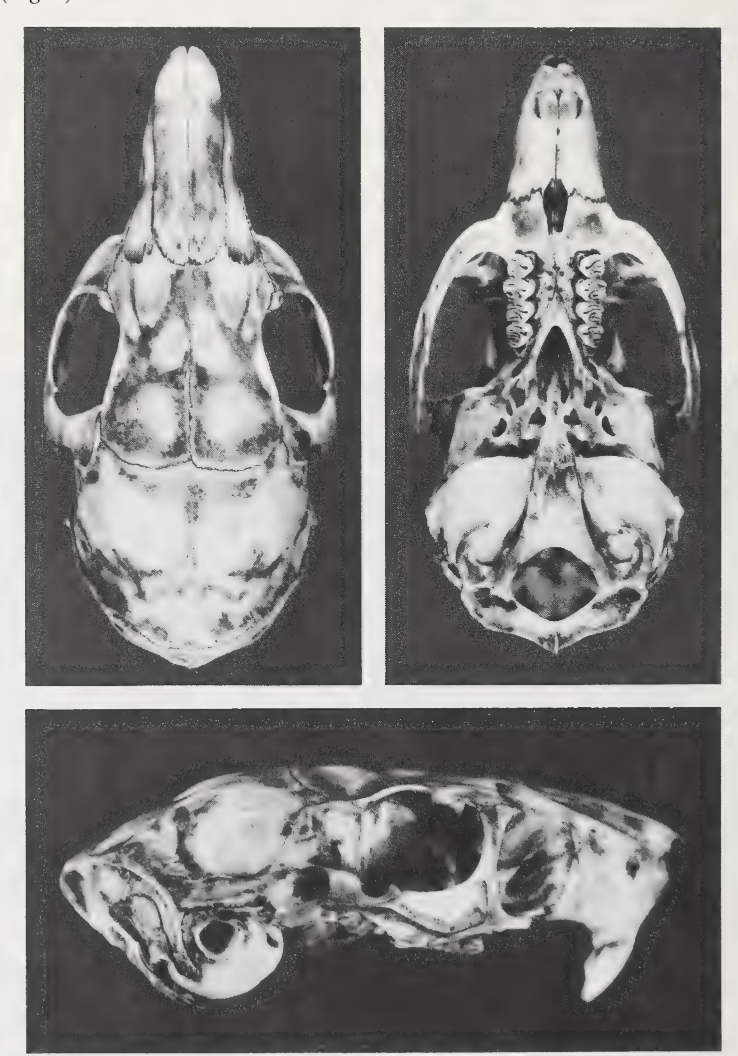


Fig. 3. Lateral, dorsal, and ventral views of the skull of the holotype of *Proechimys iheringi eliasi* (MN 30524)



Fig. 4 (left). Ventral view of the incisive foramen of the holotype of *Proechimys iheringi eliasi* (MN 30524). Premaxillae (pm), maxillae (m), and vomer (v) are indicated. – *Fig. 5 (right).* Upper left molariform teeth of the holotype of *Proechimys iheringi eliasi* (MN 30524)

Teeth: Upper premolar with one or two counterfolds, upper molars with two counterfolds; lower premolar with two counterfolds and lower molars with one counterfold (Fig. 5).

Baculum: Elongate and narrow with a straight shaft. Shaft with a slight dorsoventral curvature and a tapered lateral indentation in the proximal third. Proximal end paddle-shaped. Distal end has no apical wings or median depression (Fig. 6).



Fig. 6. Ventral (A) and lateral (B) views of the baculum of the type of *Proechimys iheringi eliasi* (MN 30524). The distal part is to the top (ventral view) and to the left (lateral view)

Table 1. **Sample sizes (N), means ($\overline{X}$), standard deviations (± SD), and minimal (Min.) and maximal (Max.) values for seventeen cranial measurements (in mm) in seven subspecies of *Proechimys iheringi***

Characters	*P. i. denigratus*				*P. i. panema*				*P. i. paratus*				*P. i. gratiosus*			
	N	$\overline{X}$ ± SD	Min.	Max.	N	$\overline{X}$ ± SD	Min.	Max.	N	$\overline{X}$ ± SD	Min.	Max.	N	$\overline{X}$ ± SD	Min.	Max.
Skull length	8	48.8 ± 2.05	46.2	52.2	5	51.1 ± 1.00	49.8	52.3	4	52.5 ± 2.18	50.3	55.5	12	50.4 ± 1.75	47.1	52.4
Basilar length	8	33.7 ± 1.42	32.0	36.5	5	35.4 ± 1.32	33.7	37.0	4	36.7 ± 1.81	34.8	38.8	12	35.3 ± 1.04	33.8	37.0
Palatal length	8	16.0 ± 1.05	14.4	17.2	5	16.7 ± 0.59	16.0	17.5	4	17.7 ± 1.15	16.5	19.2	12	16.4 ± 0.67	15.2	17.9
Toothrow length	8	7.9 ± 0.25	7.5	8.2	5	8.0 ± 0.27	7.6	8.3	4	8.5 ± 0.09	8.4	8.6	12	8.3 ± 0.58	7.6	9.8
Diastema	8	9.9 ± 0.70	8.9	11.1	5	10.7 ± 0.41	10.1	11.3	4	10.8 ± 0.50	10.5	11.5	12	10.5 ± 0.53	9.9	11.8
Rostral length	8	20.6 ± 1.16	18.5	22.5	5	21.6 ± 0.66	20.9	22.7	4	22.8 ± 0.83	21.7	23.7	12	21.6 ± 1.28	20.0	23.3
Nasal length	8	16.7 ± 0.86	15.1	17.9	5	17.9 ± 0.94	17.0	19.3	4	19.1 ± 0.62	18.4	19.9	12	17.7 ± 0.82	16.4	18.9
Interorbital constriction	8	10.7 ± 0.58	9.7	11.4	5	12.4 ± 0.82	11.3	13.4	4	11.7 ± 0.93	10.4	12.4	12	11.6 ± 0.40	10.8	12.4
Rostral breadth	8	7.6 ± 0.31	7.1	8.2	5	6.9 ± 0.59	6.1	7.8	4	6.6 ± 0.49	6.0	7.2	12	7.8 ± 0.46	7.1	8.6
Skull depth	8	12.8 ± 0.47	11.9	13.4	5	13.5 ± 0.19	13.2	13.7	4	13.2 ± 0.65	12.7	14.1	12	13.3 ± 0.53	12.4	14.3
Rostral depth	8	9.3 ± 0.44	8.7	9.9	5	10.0 ± 0.59	9.7	11.1	4	10.6 ± 0.40	10.3	11.1	12	10.3 ± 0.37	9.6	11.2
Maxillary breadth	8	8.5 ± 0.53	7.6	9.2	5	8.6 ± 0.66	7.8	9.3	4	8.3 ± 0.53	7.7	9.0	12	8.5 ± 0.53	7.7	9.4
Zygomatic breadth	8	24.9 ± 1.01	23.5	26.8	5	26.3 ± 1.37	24.7	28.0	4	25.5 ± 0.54	25.2	26.3	12	25.5 ± 0.75	24.3	26.7
Bulla length	8	9.8 ± 0.45	9.0	10.4	5	9.7 ± 0.51	9.3	10.5	4	10.6 ± 0.46	9.9	10.8	12	9.4 ± 0.60	8.5	10.3
Post-palatal length	8	23.4 ± 1.60	21.6	26.6	5	23.6 ± 1.51	21.8	25.5	4	24.2 ± 1.08	23.5	25.8	12	23.7 ± 0.79	22.5	24.9
Incisive foramen length	8	5.0 ± 0.43	4.2	5.7	5	4.7 ± 0.43	4.3	5.2	4	4.4 ± 0.16	4.3	4.6	12	5.0 ± 0.22	4.7	5.3
Mandibular length	8	24.4 ± 1.23	22.3	25.7	5	25.6 ± 1.15	24.8	27.7	4	26.6 ± 0.75	26.0	27.6	12	25.6 ± 0.95	23.7	27.1

Characters	*P. i. bonafidei*				*P. i. iheringi*				*P. i. eliasi*			
	N	$\overline{X}$ ± SD	Min.	Max.	N	$\overline{X}$ ± SD	Min.	Max.	N	$\overline{X}$ ± SD	Min.	Max.
Skull length	10	53.0 ± 2.45	49.3	56.1	6	54.8 ± 0.90	53.9	56.5	9	51.4 ± 1.86	48.8	55.4
Basilar length	10	37.0 ± 1.46	35.0	39.0	6	38.3 ± 0.81	37.4	39.5	9	35.1 ± 1.62	32.4	37.6
Palatal length	10	16.7 ± 0.98	15.3	18.2	6	18.6 ± 0.47	17.7	19.1	9	16.9 ± 0.70	15.6	18.3
Toothrow length	10	8.8 ± 0.44	8.1	9.6	6	8.4 ± 0.19	8.2	8.6	9	8.4 ± 0.36	8.0	9.1
Diastema	10	10.9 ± 0.57	10.0	11.8	6	12.2 ± 0.43	11.5	12.6	9	10.5 ± 0.48	9.7	11.5
Rostral length	10	23.3 ± 1.24	21.4	25.0	6	23.5 ± 0.90	22.9	25.3	9	22.1 ± 1.04	20.8	24.2
Nasal length	10	19.1 ± 1.14	17.2	21.0	6	20.2 ± 0.29	19.7	20.6	9	18.6 ± 0.99	16.5	19.8
Interorbital constriction	10	12.2 ± 0.55	11.5	13.1	6	12.6 ± 0.92	11.9	14.4	9	11.7 ± 0.38	11.2	12.1
Rostral breadth	10	7.8 ± 0.73	6.5	8.8	6	7.6 ± 0.27	7.3	8.0	9	7.0 ± 0.47	6.4	8.0
Skull depth	10	14.1 ± 0.35	13.5	14.8	6	14.0 ± 0.37	13.6	14.5	9	13.2 ± 0.23	12.9	13.6
Rostral depth	10	10.9 ± 0.51	10.1	11.7	6	10.8 ± 0.42	10.2	11.4	9	10.2 ± 0.49	9.8	11.2
Maxillary breadth	10	8.9 ± 0.39	8.2	9.3	6	9.5 ± 0.50	8.8	10.0	9	8.3 ± 0.55	7.4	9.2
Zygomatic breadth	10	25.8 ± 1.06	24.2	27.9	6	26.2 ± 0.89	25.3	27.7	9	25.5 ± 0.61	24.7	26.5
Bulla length	10	9.5 ± 0.59	8.3	10.6	6	10.3 ± 0.95	9.2	11.6	9	10.8 ± 0.30	10.2	11.2
Post-palatal length	10	25.0 ± 1.07	23.2	26.5	6	25.2 ± 0.39	24.6	25.7	9	23.7 ± 0.87	22.4	25.3
Incisive foramen length	10	5.2 ± 0.27	4.7	5.7	6	4.1 ± 0.43	3.5	4.7	9	5.0 ± 0.30	4.7	5.6
Mandibular length	10	26.7 ± 0.91	25.2	28.2	6	26.8 ± 1.15	25.9	29.0	9	25.9 ± 0.69	25.0	27.2



Fig. 7. Habitat of *Proechimys iheringi eliasi* at the Restinga da Barra de Maricá, State of Rio de Janeiro, Brazil

Measurements: Measurements (in mm) of the holotype are as follows: total length 410; tail 225; hindfoot 50; ear 25; skull length 55.4; basilar length 37.6; palatal length 18.3; toothrow length 8.3; diastema 11.5; rostral length 24.2; nasal length 19.8; interorbital constriction 12.1; rostral breadth 8.0; skull depth 13.1; rostral depth 11.2; maxillary breadth 7.6; zygomatic breadth 26.0; bulla length 11.2; post-palatal length 25.3; incisive foramen length 4.7; mandibular length 26.2. Means and ranges of all specimens examined are listed in Table 1.

Habitat: The coastal sand plains of the Restinga da Barra de Maricá in the State of Rio de Janeiro, are characterized by a mosaic of plant communities (Cerqueira et al. 1990). The major vegetational types can be described as meadows, scrublands, and forested slopes. Plant types in the meadows include species of the families Poaceae, Cyperaceae, Typhaceae, and Melastomataceae. The scrubs are dominated by families Myrtaceae, Erythoxylaceae, Bromeliaceae, Cactaceae, and Mimosaceae, with trees usually no higher than 4 m tall. The forested slopes have taller trees reaching 10 to 15 m, although plant species characteristic of the meadows and scrubs such as bromeliads are also present. According to Cerqueira et al. (1990), *P. i. eliasi* occurs primarily in the scrubs shown in Figure 7.

Etymology: The epithet *eliasi* honors the memory of Prof. Elias Pacheco Coelho whose pioneer work made possible the training of young zoology students at the Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil.

Discussion

The taxonomy of *P. iheringi* was established by Moojen (1948), who described the subspecies as part of a broader study of the Brazilian forms of spiny rats of the subgenera

Proechimys and *Trinomys*. For each subspecies, MOOJEN (1948) described the color and thickness of aristiform and setiform hairs, and provided descriptions of several qualitative aspects of skull morphology, which included (1) the size and shape of the bullae, (2) degree of develoment of ridges and depth of jugal bone, (3) degree of development of post-orbital process of zygoma, (4) shape and anatomy of the incisive foramen, and (5) placement of posterior palatine foramina. MOOJEN (1948) also detailed variation in the number of counterfolds in upper and lower molariform teeth.

Although MOOJEN (1948) described variation in the characters listed above, he found diagnostic features to define the geographic units of *P. iheringi* primarily among tail length relative to body size, thickness of aristiforms and color patterns of setiform hairs, morphology of incisive foramen, and pattern of counterfold in molariform teeth. These traits have also proven useful to characterize and distinguish *P. i. eliasi* from the other subspecies of *P. iheringi*. The tail is longer than head and body in *P. i. eliasi* and *P. i. denigratus*, shorter than head and body in *P. i. iheringi, P. i. bonafidei,* and *P. i. paratus* and is about the same length as head and body in *P. i. gratiosus* and *P. i. panema*. *Proechimys i. eliasi* and *P. i. denigratus* share a whitish brush in the tail tip.

The aristiforms on the dorsal region are wider in *P. i. eliasi* (1.1 mm) than in *P. i. iheringi* (0.6 mm), *P. i. bonafidei* (0.8 mm), *P. i. gratiosus* (0.6 mm), and *P. i. panema* (0.8 mm). The aristiforms in *P. i. eliasi* have about the same width as in *P. i. denigratus* (1.1 mm), whereas *P. i. paratus* has the widest aristiforms (1.3 mm). The color pattern of setiform hairs also differs noticeably in *P. i. eliasi*. In all subspecies of *P. iheringi* described by MOOJEN (1948), the setiform hairs on middorsal region are interrupted by a Cinnamon or Ochraceous subapical zone. Such Cinnamon or Ochraceous subapical zone is lacking in *P. i. eliasi* and imparts a dark color pattern to the dorsum, which makes the pelage of the new subspecies very distinctive from the other subspecies of *P. iheringi*.

MOOJEN (1948) recognized the shape and dimensions of the incisive foramen as diagnostic characters to define taxa at specific and infraspecific levels in the subgenus *Trinomys* (reviewed in PESSÔA [1992]). The incisive foramen is elongate and always constricted posteriorly in *P. iheringi*, although the morphology of the septum that crosses the incisive foramen provides diagnostic features for the recognition of the subspecies. The septum is formed by processes of premaxillary and maxillary bones. The premaxillary portion is usually well developed, whereas the length and width of the maxillary portion vary considerably. The premaxillary and maxillary parts can be either in direct contact or separate. The former condition was described as complete and the latter as incomplete by MOOJEN (1948). Finally, the vomer may be exposed ventrally between the premaxillary and maxillary portions of the septum. All such conditions can be seen in the subspecies of *P. iheringi*. The septum is complete and formed by premaxillary and maxillary portions in *P. i. paratus, P. i. iheringi,* and *P. i. bonafidei*. The maxillary portion is well developed in *P. i. paratus* and in *P. i. iheringi,* and is thin and delicate in *P. i. bonafidei*. The septum in *P. i. gratiosus* and *P. i. panema* is formed by premaxillary and maxillary portions, but it is incomplete since the maxillary portion is reduced to a small process. In *P. i. eliasi* and *P. i. denigratus* the septum is also complete, but the vomer is visible ventrally between the premaxillary and maxillary portions.

MOOJEN (1948) evaluated the usefulness of the number and pattern of folds in the molariform teeth, and was able to demonstrate that the length of the main fold is a most trenchant character to define the morphological limits of subgeneric variation in *Proechimys*. The analysis of variation in the number of counterfolds at the specific and subspecific levels is hampered, however, as folds can become obliterated or coalesce with increasing age (MOOJEN 1948). Variation in the number of counterfolds thus has to be addressed with caution given the caveat of age-related modification. Inspection of MOOJEN's (1948) description of the number of folds in subspecies of *P. iheringi* indicates moderate variation, primarily due to coalescence of folds. Nevertheless the presence of two

folds is relatively common in *P. i. gratiosus, P. i. panema, P. i. paratus, P. i. bonafidei*, and *P. i. eliasi*. On the other hand, *P. i. iheringi* can have up to four folds, whereas in *P. i. denigratus* the number of folds can be reduced to one.

The degree of development as well as the bones that contribute to the formation of the post-orbital process of zygoma were described by Moojen (1948), but not featured in the subspecific diagnoses of *P. iheringi*. This structure nevertheless does contribute to characterize the subspecies and is considered here. The post-orbital process of zygoma is small and formed only by the squamosum in *P. i. gratiosus* and *P. i. panema*, mostly by the squamosum in *P. i. bonafidei* and by both jugae and squamosum in *P. i. iheringi*. In *P. i. eliasi* and *P. i. denigratus* the post-orbital process is formed almost exclusively by the jugae, although is only moderately developed in the former and spiniform in the latter. In *P. i. paratus* the post-orbital process is moderately developed and formed by the squamosum only.

Variation in cranial dimensions in all subspecies of *P. iheringi* is summarized in Table 1. *Proechimys i. eliasi, P. i. panema*, and *P. i. gratiosus* are similar in average skull size. *Proechimys i. eliasi* is smaller in average skull size than the other subspecies of *P. iheringi*, with the exception of *P. i. denigratus*. In contrast, *P. i. eliasi* has the largest mean value for bulla length. The larger size of the bulla of the new subspecies can be appreciated by a comparison with mean bullae and skull length values for *P. i. bonafidei* and *P. i. iheringi*. These two subspecies are geographically the closest to *P. i. eliasi* and, while they have average skulls larger than *P. i. eliasi*, their mean values for bulla length are smaller. *Proechimys i. denigratus* is the only other subspecies whose bulla is equally large relative to cranial size.

Acknowledgements

We thank the curators at the Museu Nacional and Museu de Zoologia da Universidade de São Paulo for allowing the study of specimens under their care. We are deeply indebted to M. F. Pessôa for the drawings and technical support throughout the development of this project. Research supported by grants from Fundação de Amparo à Pesquisa do Estado do Rio de Janeiro (E-29/170.339/90), Fundação de Amparo à Pesquisa do Estado de São Paulo (88/2237-4, 89/0772-1, and 89/3405-0), and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNP_q) (400052/91-1[NV]). Work by LMP and SFR is partially supported by Programa de Incentivo à Capacitação Docente, Universidade Federal do Rio de Janeiro and CNPq, respectively.

Zusammenfassung

Eine neue Unterart von Proechimys iheringi (Rodentia: Echimyidae) aus dem Bundesstaat Rio de Janeiro, Brasilien

Aus den sandigen Küstenebenen des Bundesstaates Rio de Janeiro (Brasilien) wird eine neue Unterart von *Proechimys iheringi* beschrieben. Sie ist durch eine Kombination von Merkmalen gekennzeichnet, unter denen das Fehlen einer zimtfarbenen Zone im subapikalen Bereich des Haarkleides, ein mehr als körperlanger Schwanz mit einem terminalen weißen Pinsel, große Ohrblasen im Schädel und morphologische Details des Septums zwischen den Foramina incisiva besonders charakteristisch sind.

Literature

Cerqueira, R.; Fernandez, F. A. S.; Quintela, M. F. S. (1990): Mamíferos da restinga de Barra de Maricá, Rio de Janeiro, Papéis Avulsos Zool. **37**, 141–157.

Moojen, J. (1948): Speciation in the Brazilian spiny rats (Genus *Proechimys*, Family Echimyidae). Univ. Kans. Publ. Mus. Nat. Hist. **1**, 301–401.

Pessôa, L. M. (1989): Diferenciação craniana infraespecífica em *Proechimys iheringi* Thomas e *Proechimys dimidiatus* (Günther) (Mammalia: Rodentia: Echimyidae). Unpubl. M. Sc. Diss. Univ. Federal do Rio de Janeiro, RJ.

— (1992): Variação morfológica, taxonomia e sistemática do subgênero *Trinomys*, gênero *Proechimys* (Rodentia: Echimyidae). Unpubl. D. Sc. Diss. Universidade Estadual Paulista, SP.

PESSÔA, L. M.; REIS, S. F. (1991): Cranial infraspecific differentiation in *Proechimys iheringi* Thomas (Rodentia: Echimyidae). Z. Säugetierkunde **56**, 34–40.
REIS, S. F.; PESSÔA, L. M.; BORDIN, B. (1992): Cranial phenotypic evolution in *Proechimys iheringi* (Rodentia: Echimyidae). Zool. Scr. **21**, 201–204.
RIDGWAY, R. (1912): Color standards and color nomenclature. Washington: Published by the author.
THOMAS, O. (1911): New rodents from South America. Ann. Mag. Nat. Hist. ser. 8, **8**, 252–253.

Authors' addresses: LEILA MARIA PESSÔA, Departamento de Zoologia, IB, Universidade Federal do Rio de Janeiro, 21941 Rio de Janeiro, RJ, Brazil; SÉRGIO F. DOS REIS, Departamento de Parasitologia, IB, Universidade Estadual de Campinas, 13081 Campinas, SP, Brazil

Z. Säugetierkunde 58 (1993) 191–193

ISSN 0044-3468

WISSENSCHAFTLICHE KURZMITTEILUNGEN

Biometrics of the digestive tract of three species of Ctenodactylidae: comparison with other rodents

By P. Gouat

Laboratoire d'éthologie, Université C. Bernard, Lyon, France

Receipt of Ms. 1. 6. 1992
Acceptance of Ms. 6. 11. 1992

There are two major problems for rodents living in a hot desert. Firstly, high temperatures and secondly, the scarcity of water which necessitates a very careful conservation of body fluids. For these reasons, the majority of small mammals living in the Sahara desert are nocturnal (Happold 1984). One of the major exceptions to this are the gundis (*Ctenodactylus gundi, Ctenodactylus vali* and *Massoutiera mzabi*) which are diurnal (Gouat 1991). These species are primarily herbivorous (Gouat 1988). Grenot (1974) has suggested that gundis possess a very powerful renal function in order to maintain their water balance in equilibrium. The physiological studies performed on *C. vali* (Rouffignac et al. 1981) and *M. mzabi* (George 1987) have not shown major anatomical or physiological renal adaptations in these species when compared with other desert rodents. As suggested by George (1987), behavioural adaptations to temperature do exist but they are not sufficient to explain how these species can survive in an arid climate (Gouat 1991).

Considerable amounts of water may be lost with the faeces. As compared with other rodents and as a general rule, desert rodents emit dry faecal pellets (Ghobrial and Nour 1975). In fact, gundis defaecate very dry pellets (Gouat 1992), and this study suggests that water absorption along the large intestine is very important. The hypothesis concerning an adaptation of the digestive tract of ctenodactylids for this purpose was tested by an anatomical study. This study included comparisons with other rodents: a laboratory herbivorous rodent, the guinea pig (*Cavia porcellus*) and two omnivorous nocturnal rodents, *Meriones libycus*, a desert rodent, and *Meriones shawi*, a rodent living in a less arid climate (Petter 1961).

Animals were kept in the laboratory before being sacrificed for dissection. The specimens of *C. gundi, M. shawi, M. libycus* and *C. porcellus* were bred in the laboratory. The specimens of *C. vali* were captured in the Saoura basin (Algeria), and those of *M. mzabi* were collected in the Mzab (Algeria). The body length (measured from tip of nose to base of tail) of all specimens was determined prior to dissection. The mesentery was removed and the intestines unwound and placed outside the abdominal cavity. A photograph with two orthogonal scales was taken of each dissection. The lengths of three different sections were measured: the small intestine (from stomach to caecum); the caecum; the large intestine (from caecum to anus). Each intestinal section was measured from the picture using a curvometer adjusted by means of the two scales. The total length of the gut is defined as the sum of large and small intestine plus caecum. The number of animals used and absolute intestinal measurements are presented in table 1.

To allow for direct comparisons, these measurements were transformed into relative proportions (Perrin and Curtis 1980). Figure 1 shows the combination of the two most pertinent values of the analysis: relative total length of the gut as a proportion of body

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5803-0191 $ 02.50/0

Table 1. **Biometrics of the gut of five species of rodents**
All lengths are given in cm

		BL	LI	CA	SI
Ctenodactylus gundi	mean	18.41	91.97	13.20	65.35
N = 15	S.D.	3.25	20.41	3.05	16.28
Ctenodactylus vali	mean	14.90	81.13	10.37	51.73
N = 6	S.D.	1.97	13.97	3.75	6.08
Massoutiera mzabi	mean	18.33	95.73	12.13	42.72
N = 6	S.D.	1.14	17.23	1.74	16.02
Cavia porcellus	mean	24.98	91.77	14.31	143.66
N = 9	S.D.	4.16	17.87	3.88	2.72
Meriones libycus	mean	14.35	25.78	8.23	41.63
N = 6	S.D.	1.16	4.30	1.01	2.72
Meriones shawi	mean	15.46	21.80	7.06	46.39
N = 8	S.D.	0.69	2.55	0.57	5.77

BL = body length; SI = small intestine length; CA = caecum length; LI = large intestine length.

length; large intestine length expressed as a percentage of total length of the gut. Each symbol represents an animal. The horizontal line B divides the symbols into two groups according to their relative large intestine length. The two *Meriones* species and the guinea pigs are found below line B whilst the three species of gundis are found above line B. Statistical comparisons of the relative large intestine length between the species of the two groups are highly significant (two-tailed t test, $p < .001$ for each species/species comparisons). Clearly the gundis have proportionally a longer large intestine than the other rodents. Differences are found between the three species of gundis, *C. gundi*, the species living in a less arid climate, has proportionally a shorter large intestine (m = 53.9 %) when

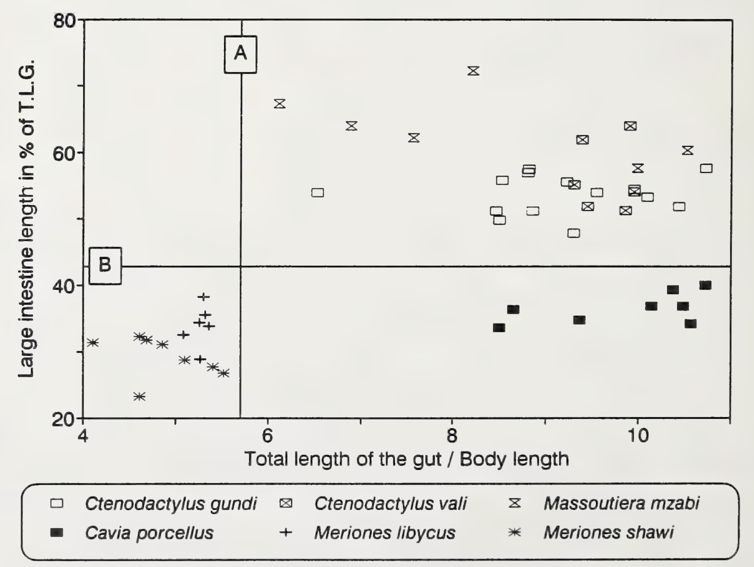


Fig. 1. Comparison of relative total length of the gut and of relative large intestine length of five species of rodents

compared with the two desert species *C. vali* (m = 56.3 %) or *M. mzabi* (m = 64.0 %). The differences between *M. mzabi* and each of the two species of *Ctenodactylus* are significant (two-tailed t test, $p < .05$ for each comparison). A similar difference is found between the two species of *Meriones, M. libycus*, the desert species, having a relatively longer intestine than *M. shawi* (respectively, m = 33.9 % and m = 29.1 %; $p = .018$, two tailed t test). The vertical line A divides the symbols into two groups of species. On the left the two *Meriones* species are found; both of them are omnivorous species with a short gut. On the right side a group of herbivorous species is found with a long gut, including the three species of gundis and the guinea pigs. It is interesting to note that gundis have proportionally a longer large intestine than both other types of rodents. These results are arguments for an adaptation of the large intestine to an arid climate. Nevertheless, "morphology is just one of several features upon which natural selection has operated in the evolution of different digestive system" (Karasov 1988). Cytological and physiological studies are required to confirm the role of the large intestine in water absorption in the gundis.

References

Ghobrial, L. I.; Nour, T. A. (1975): The physiological adaptations of desert rodents. In: Rodents in desert environments. Ed. by I. Prakash and P. K. Ghosh. The Hague: DR. W. Junk bv Publishers. Pp. 413–444.

George, W. (1987): *Massoutiera mzabi* (Rodentia, Ctenodactylidae) in a climatological trap. Mammalia **52**, 331–338.

Gouat, P. (1988): Etude socioécologique de trois espèces de rongeurs Cténodactylidés d'Algérie. Thèse d'état, Université C. Bernard, Lyon.

Gouat, P. (1991): Adaptation comportementale à la température chez trois espèces de Cténodactylidés sahariens. In: Le rongeur et l'espace. Ed. by M. Le Berre and L. Le Guelte. Paris: R. chabaud. Pp. 79–89.

Gouat, P. (1992): Faecal pellet size differences as a field criterion to distinguish between the two Ctenodactylus species (Mammalia, Rodentia). Z. Säugetierkunde **57**, 183–185.

Grenot, C. (1974): Sur la biologie d'un rongeur héliophile du Sahara, le "goundi" (Ctenodactylidae). Acta Tropica **30**, 237–250.

Happold, D. C. (1984): Small mammals. In: Sahara desert. Ed. by J. L. Cloudsley-Thompson. Oxford: Pergamon Press. Pp. 251–275.

Karasov, W. H. (1988): Nutrient transport across vertebrate intestine. In: Advances in Comparative and Environmental Physiology. Ed. by G. A. Ahearn. Berlin: Springer-Verlag. Vol. **2**, 131–172.

Perrin, M. R.; Curtis, B. A. (1980): Comparative morphology of the digestive system of 19 species of Southern African myomorph rodents in relation to diet and evolution. S.-Afr. Tydskr. Dierk. **15**, 22–33.

Petter, F. (1961): Répartition géographique et écologie des rongeurs désertiques de la région paléartique. Mammalia **25**, 1–219.

Rouffignac, C. de; Bankir, L.; Roinel, N. (1981): Renal function and concentrating ability in a desert rodent: the gundi (*Ctenodactylus vali*). Pflügers Arch **390**, 138–144.

Author's address: Patrick Gouat, L. E. E. C., URA 667, Université Paris Nord, F-93430 Villetaneuse, France

Z. Säugetierkunde 58 (1993) 194–196

ISSN 0044-3468

A dental peculiarity in *Numidotherium koholense*: evidence of feeding behaviour in a primitive proboscidean

By N. Court

Sedgwick Museum, Department of Earth Sciences, University of Cambridge, Cambridge, U.K.

Receipt of Ms. 19. 9. 1991
Acceptance of Ms. 27. 12. 1992

The fossil proboscidean, *Numidotherium koholense* is known only from the Palaeogene of Algeria (Mahboubi et al. 1984). Abundant remains of this tapir-sized mammal have been recovered from a single locality at El Kohol in Eocene deposits of the Southern Atlas of Algeria (see Mahboubi et al. 1986 for site details). The late Early Eocene age ascribed to this locality renders *Numidotherium* the oldest unequivocal representative of the order Proboscidea yet known. Material includes numerous isolated teeth, jaws and skulls, in addition to postcranial elements. Although *Numidotherium* is morphologically well documented (Mahboubi et al. 1986) and has been included in recent phylogenetic treatments of the order (Tassy 1990), as yet nothing is known of numidothere life habits or autecology.

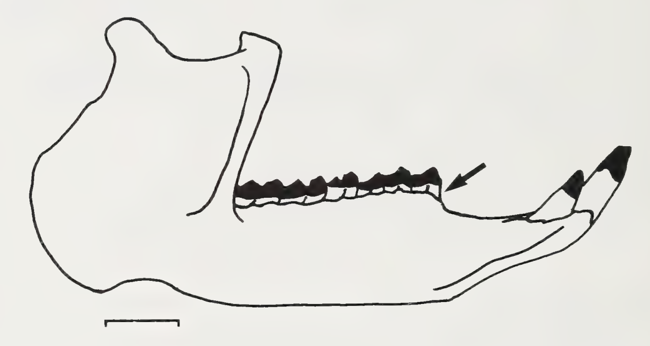


Fig. 1. Outline drawing of right mandibular ramus of *Numidotherium koholense* in lateral view. Note the long diastema and the way in which the alveolar border in front of P2 descends steeply to expose the anterior root (arrow). Modified from Mahboubi et al. 1986). Scale = 50 mm

The first tooth in the mandibular postcanine dentition (P2) is morphologically simple, consisting of a single high anterior cusp and a low distal heel; it is the wear on this tooth that forms the subject of the following communication. The mandibular dental formula consists of two incisors, three premolars and three molars, each of the latter bearing two cross-crests indicating a diet of herbivorous brows. The mandible is robust with enlarged incisors projecting anteriorly and slightly dorsally from a long synostosed symphysis. A substantial diastema occurs between the first premolar (P2) and the incisors, the free alveolar border descending quite steeply from P2 to the enlarged incisors (Fig. 1). Crown wear on P2 is unremarkable and clearly related to normal tooth-food-tooth interactions during mastication; however the most peculiar feature of this tooth occurs on the anterior root. Situated on the anterobuccal side of the anterior root just below the crown enamel there is a deep but smooth notch-like excavation (Fig. 2). The deepest part of this

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5803-0194 $ 02.50/0

depression is located just below the crown and trends posterobuccally and slightly dorsally. Viewed under the binoccular microscope this excavation is seen to be covered in fine parallel striations trending posterodorsally. There can therefore be little doubt that this is a wear induced feature. Tooth wear and dental function are generally well understood in herbivorous mammals (Fortelius 1985); however, wear in this position on a tooth is certainly anomalous. Had the illustrated tooth (Fig. 2) been the only example exhibiting this peculiarity it might then have been explicable in terms of some form of dental pathology leading to malocclusion. Further investigation, however, revealed that this facet occurs, to varying degrees, on all lower P2's, both left and right where this part of the tooth is preserved. This peculiarity pertains only to the anterior-most lower premolar and has not been found to occur at any other locus within the postcanine dentition.



Fig. 2. A, KA 185, Stereophotograph left lower P2 of *Numidotherium koholense* in anterior view. B, KA 185 Stereophotograph of left lower P2 in buccal view. A wedge shaped excavation can be seen on the anterobuccal surface of the anterior root. Arrows show the direction of striations on the surface of this feature and indicate that is the result of food abrasion. Scale = 5 mm

The inevitable conclusion is that this pattern of root abrasion has resulted from some aspect of the habitual feeding behaviour in numidotheres and is not a phenomenon restricted to aberrant individuals. Moreover, it is impossible that such root wear could have resulted from normal tooth-food-tooth interactions during mastication. The only plausible cause of wear in this position is that of abrasion caused during food procurement. Since jaw movement relative to the abrasive food-stuff is likely to be the cause of this particular feature, the fact that the depression and striations upon it are orientated from anterolingual to posterobuccal and incline posteriorly (Fig. 2) indicates that the relative direction of causative jaw movement was orientated ventrolaterally.

How then might this pattern of wear have occurred? The most likely explanation is that fibrous plant material was secured within the oral cavity, either between the teeth on one side of the jaw, or by pressures applied by the tongue. The head was then forcibly rotated in a ventrolateral direction. Such a head movement would cause the plant material to slide unobstructed across the mandibular diastema until it came up against the anterior tooth in the premolar row on that side of the jaw opposite the direction of head movement. As noted above the alveolar border in front of the anterior-most premolar descends steeply such that the anterior root of P2 stands proud of the alveolar bone (Fig. 1). The result is that this part of the tooth becomes abraded during the described behaviour. A very similar pattern of dental wear in the European cave bear *Ursus spelaeus*, has been interpreted as evidence of herbivory in this carnivore (Breuer 1933).

This straightforward observation illuminates at least one aspect of food procurement behaviour in the earliest or proboscideans, and indicates that *Numidotherium* likely specialised on brows occurring at or above head height. Finally, since bilophodonty is associtaed with the comminution of leaves, it is not inconceivable that numidotheres utilised the described behaviour to strip leaves from slender branches.

Acknowledgements

Thanks to Prof. J.-J. Jaeger for allowing me facilities and access to material. Drs. M. Fortelius and J. Shoshani kindly commented on my observations. Dr. F. v. Mering kindly provided a translation of Breuer (1933).

References

Breuer, G. (1933): Über das Vorkommen sog. keilförmiger Defekte an den Zähnen von *Ursus spelaeus* und deren Bedeutung für die Palaeobiologie. Palaeobiologica **5**, 103–144.
Fortelius, M. (1985): Ungulate cheek teeth: developmental, functional and evolutionary interrelations. Acta zoologica Fennica **180**, 1–76.
Mahboubi, M.; Ameur, R.; Crochet, J. Y.; Jaeger, J. J. (1984): The earliest known proboscidean from north-west Africa. Nature **308**, 43–544.
Mahboubi, M.; Ameur, R.; Crochet, J. Y.; Jaeger, J. J. (1986): El Kohol (Saharan Atlas, Algeria): a new Eocene mammal locality in Northwestern Africa. Palaeontographica, Abt. A. **192**, 15–49.
Tassy, P. (1990): Phylogénie et classification des Proboscidea (Mammalia): historique et actualité. Annales de Paléontologie **76**, 159–224.

Author's address: Dr. Nick Court, Sedgwick Museum, Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge, CB2 3EQ. U.K.

AG Tiergartenbiologie

Nachdem im vergangenen Jahr auf der Tagung in Karlsruhe die Einrichtung von Arbeitsgruppen beschlossen wurde, ist auf Betreiben von Herrn Dir. Dr. H. Frädrich, Zoo Berlin, und PD Dr. Ganslosser, Zool. Institut Erlangen, eine Arbeitsgruppe Tiergartenbiologie gegründet worden. Diese Gruppe wird auch bei den Mitgliedern der Ethologischen Gesellschaft propagiert und hat dort bereits große Resonanz ausgelöst.

Ziel soll nicht die Durchführung jeglicher Art von Forschung im Zoo sein, sondern die Diskussion und ggf. Erarbeitung von Konzepten und Projekten für und mit den Zoos zur Lösung spezifischer Probleme bei Haltung und Zucht seltener Arten.

Durch die Mitgliedschaft des Zweitunterzeichneten in verschiedenen Gremien der Europäischen Zoo- und Zuchtbuchorganisationen ist ein enger Kontakt zu diesen und den „Praktikern" gewährleistet. Interessenten werden gebeten, sich an folgende Adresse zu wenden:
PD Dr. Udo Ganslosser, Zoologisches Institut 1, Staudtstr. 5, D-91058 Erlangen.
Ein erster Workshop soll am Wochenende 28./29. August 1993 in Erlangen stattfinden.
Über umfangreiche Reaktionen würden sich freuen

gez. Dir. Dr. H. Frädrich
Zoo Berlin

gez. PD Dr. U. Ganslosser
Zool. Institut 1, Erlangen

Arbeitskreis „Wirbeltiere" der Deutschen Phytomedizinischen Gesellschaft

Am 5. und 6. Oktober 1993 findet in Bad Zwischenahn das 6. Jahrestreffen des Arbeitskreises „Wirbeltiere" der Deutschen Phytomedizinischen Gesellschaft statt.

Diese 1988 gegründete AG versteht sich als Informations- und Diskussionsforum für den Bereich der angewandten Wirbeltierforschung, insbesondere der Säugetierkunde.

Schwerpunktmäßig sollen Fragen der Biologie und Ökologie im land- und forstwirtschaftlichen Bereich heimischer Arten diskutiert werden.

Die Tagung in Bad Zwischenahn beginnt am 5. 10. um 13.00 Uhr und endet am 6. 10. um ca. 18.30 Uhr. Für den Nachmittag des 6. 10. ist eine Exkursion vorgesehen (Thema: Schäden durch Feldmaus und Bisam und deren Abwehr).

Der Arbeitskreis steht insbesondere auch jungen Interessenten offen und bietet die Gelegenheit, aus eigenen Arbeiten zu berichten.

Für nähere Informationen wenden Sie sich bitte an:
Dr. Hans-Joachim Pelz, Biologische Bundesanstalt für Land- und Forstwirtschaft, Institut für Nematologie und Wirbeltierkunde, Toppheideweg 88, D-48161 Münster, Tel. 02 51/8 60 18

BUCHBESPRECHUNGEN

Fischer, M. S.: **Hyracoidea.** Handbuch der Zoologie. Bd. VIII: Mammalia, Teilb. 58. Berlin und New York: De Gruyter 1992. 169 S., 121 Abb., 8 Tab. Geb. DM 360,–. ISBN 3-11-012934-5

Eine vorzügliche Monographie über die Säugetierordnung der Hyracoidea ist anzuzeigen: Martin S. Fischer, Tübingen, und der Verlag legten ein Werk vor, welches durch die Vielfalt der Aspekte, unter denen die Schliefer behandelt werden, beeindruckt. Beim Leser wird auch die Dichte der gebotenen Informationen und die klare und schnörkellose Sprache Anerkennung finden. Die informative Bebilderung ist sorgfältig ausgewählt und der Satzspiegel großzügig.

Nach einer kurzen Einführung in die Geschichte der Erforschung der Schliefer wird in den folgenden Abschnitten die Stellung der Hyracoidea im System behandelt, dann werden ihre Stammesgeschichte und ihre taxonomischen Besonderheiten diskutiert. Bei diesen Darstellungen kann der Verfasser häufig auf seine eigenen grundlegenden Studien zurückgreifen. Im folgenden Kapitel wird die Verbreitung von insgesamt acht Arten innerhalb der drei Gattungen *Procavia, Heterohyrax* und *Dendrohyrax* geschildert. Die Aussagen werden durch eine Karte und durch eine ausführliche Liste mit Verbreitungsnachweisen rezenter Procaviiden ergänzt. Reizvoll ist eine ausführliche Liste der Namen, mit welchen verschiedene Ethnien Afrikas, des Nahen Ostens und Arabiens die Schliefer bezeichnen.

Den größten Abschnitt des Buches (78 S.) nimmt die Schilderung der Morphologie der Hyracoidea ein. Osteologie, makroskopische wie mikroskopische Anatomie, in vielen Fällen auch funktionellanatomische Befunde, werden bei diversen Organsystemen unter vergleichenden Gesichtspunkten abgehandelt. Auch in diesem Abschnitt kann der Autor auf eigene Untersuchungen verweisen. Es fällt die Sorgfalt auf, mit welcher der Verfasser die zahlreichen eigenen Abbildungen (Zeichnungen und Photos) durch aus der Literatur übernommene Darstellungen ergänzt. Sein Buch ist trotz der Vielfalt der von ihm verwendeten Vorlagen in einheitlichem Stil illustriert. Bei den von Fischer selbst entworfenen Abbildungen fällt die Benutzung von logischen und leserfreundlichen Abkürzungen für die Beschriftung der markierten Strukturen angenehm auf.

Die Implantation des Keimlings im Uterus sowie die Besonderheiten der fetalen Membranen, der Plazentation und der Karyotypen der Schliefer werden besprochen und anschließend auf etwa 25 Seiten die Verhaltens- und Fortpflanzungsbiologie von *Procavia, Heterohyrax* und *Dendrohyrax* behandelt. Dabei handelt es sich nicht um Wiederholungen der bereits früher im Handbuch der Zoologie von U. Rahm publizierten Studien zum Verhalten der Schliefer oder um kursorische Ergänzungen; es wird vielmehr der inzwischen beträchtlich erweiterte Wissensstand dargestellt.

In tabellarischer Form und mit kurzen Bemerkungen vermittelt ein weiteres Kapitel einen Eindruck von der Vielfalt der Parasiten, welche bisher bei Schliefern gefunden worden sind. Kurze Abschnitte über die wirtschaftliche Bedeutung der Hyracoidea und über den Gefährdungsstand der beiden Arten *Dendrohyrax arboreus* und *D. validus* schließen den Textteil des Bandes ab.

Der Wert dieses Werkes wird durch die Liste der in ihm verarbeiteten Publikationen eindrucksvoll belegt: Das Literaturverzeichnis beansprucht 16 Seiten, wobei auf jeder Seite etwa 50 Zitate zu finden sind! Ferner werden die in diesem Werk gebotenen Informationen nicht nur durch ein sehr ausführlich untergliedertes Inhaltsverzeichnis, sondern auch durch einen abschließenden Index zugänglich gemacht.

Wer in Zukunft über die Hyracoidea arbeiten will oder Informationen zur Biologie dieser hochinteressanten Säugetierordnung sucht, wird „den Fischer" nicht unberücksichtigt lassen können!

P. Langer, Gießen

Teerink, B. J.: **Hair of West European mammals: atlas and identification key.** Cambridge: Cambridge University Press 1991. 224 pp., 284 figs., and 73 plates. £ 35.00. ISBN 0-521-40264-6

Die Bestimmung von isolierten Haaren aus Mageninhalten, Kotballen, Gewöllen oder Nestern ist eine wichtige Methode für biologische Untersuchungen an Säugetieren und Vögeln. Der vorliegende Atlas ist als Hilfsmittel für derartige Studien konzipiert. Er illustriert beispielhaft die lichtmikroskopisch erfaßbare Morphologie der Körperhaare von 73 mitteleuropäischen Säugetierarten von *Erinaceus europaeus* bis *Ovis musimon*. Der Autor gibt zunächst eine kurze Einführung in den Vorgang der Haarentwicklung, beschreibt dann die Grob- und Feinmorphologie von Kutikula, Cortex und Medulla in Aufsicht und im Querschnitt und weist den Leser schließlich in die von ihm angewandten Präparationsmethoden ein. Für jede Familie, insgesamt 12, werden Bestimmungsschlüssel geboten, die mit 228 Strichzeichnungen illustriert sind. Den Hauptteil des Buches bilden 73 Fototafeln, die in der Regel Leit-, Grannen- und Wollhaare in bis zu 11 verschiedenen Querschnitten und Kutikularansichten zeigen. Eine Liste der wissenschaftlichen Namen und der entsprechenden Trivialnamen in

englischer, deutscher, französischer, niederländischer und dänischer Sprache sowie ein kurzes Literaturverzeichnis beschließen das Werk.

Der Atlas besticht durch seine sorgfältige und konsequente Ausführung und durch anschauliche und teilweise originelle Illustrationen. Man sieht dem Buch die Zeit und Mühe an, die seine Herstellung gekostet hat. Es kann wohl mit gutem Grund als das Referenzwerk für die Bestimmung von Haarproben mitteleuropäischer Säuger angesehen werden. R. Hutterer, Bonn

Reuther, C.; Röchert, R. (eds.): **Proceedings V. International Otter Colloquium.** Habitat Vol. 6. Hankensbüttel, Germany: Gruppe Naturschutz 1991. 344 pp., 132 figs. DM 45,–. ISBN 3-927 650-08-0

In September 1989 the Vth International Otter Colloquium was held at the Otterzentrum in Hankensbüttel, Germany. 130 scientists and specialists in the biology of otters from 36 countries met at this occasion to outline and discuss certain problems of nature and species conservation. Most of the oral presentations have been compiled in these proceedings.

The various reviews and special reports are arranged under the following headings: Status reports; biology of Lutrinae; monitoring otter distribution; causes of decline/conservation strategies; otters in captivity; education. In a concluding chapter, resolutions and some information on the activities of the IUCN/SSC otter specialist group are given, and their local officials are listed. The programme of the meeting and the list of participants (with addresses) and sponsors are included in an appendix.

Although mainly dealing with the species *Lutra lutra,* interesting new data of other lutrines from the Americas, Africa, and Asia are also mentioned. The information included in these proceedings is unfortunately rather scattered. Some contributions handle their theme very critically and accurately, while others do so in a rather superficial manner. However, this book is a reliable source on the biology and distribution of lutrines and on what is going on with these mammals worldwide.

D. Kruska, Kiel

Redford, K. H.; Eisenberg, J. F.: **Mammals of the Neotropics.** Vol. II: The Southern Cone. Chile, Argentinia, Uruguay, Paraguay. Chicago, London: University of Chicago Press 1992. 430 pp., num. ill., num. tabs. Cloth: US$ 109.25; ISBN 0-226-70681-8; paper: US$ 45.50; ISBN 0-226-70682-6

The second volume of a remarkable work has been published and a wealth of information on the mammals of Chile, Argentinia, Uruguay, and Paraguay is now available. John F. Eisenberg, the author of the first volume, invited Kent H. Redford of the University of Florida in Gainesville to co-author this volume.

Short introductory remarks are followed by "An introduction to the biogeography of southern South America". Together with four maps the political, geographical and ecological differentiations of the Southern Cone of the continent are introduced with consideration of the climate and vegetation.

From page 14 to page 406 mammals belonging to 10 terrestrial and one marine (Cetacea) order are dealt with. The authors follow a strict format in these descriptions: They start with a diagnosis of the order, give a short discription of its distribution and comment on its palaeontological history, as well as on its classification. After this follows a diagnosis, a description of the distribution and remarks on the natural history of mammalian families. On a third level a general description, the characterisation of geographical distribution, as well as life history and ecology of the genera is presented and followed by a detailed description of those species of the genus that live in southern South America. In most cases the presentation of each species is subdivided into a list of body measurements, a general description, characterisation of its distribution, which is always accompanied by a map, and, finally, by data on the species' life history and ecology.

As both authors have performed mammological field work in South America, they can deal competently with mammalian community ecology in a chapter of 12 pages that follows the description of mammals. Amongst other subjects, the authors present a short synopsis of some mammal communities and the predator influence on mammals. The effect of introduced mammals, as well as plant-animal interactions in southern South America are briefly discussed. A final chapter informs the reader about the effect of humans on the mammalian fauna of that part of the continent. Each chapter closes with an extensive list of references. 18 plates by Fiona Reid illustrate the habitus and – on eight plates – the colouration of the considered species. At the end of the book two indexes of scientific names as well as English and Spanish common names help the reader to make efficient use of this highly valuable publication.

For the non-South American reader the information is fascinating, especially for those mammals that represent a considerable and characteristic proportion of the fauna of the temperate part of the continent, such as Marsupialia, Xenarthra (Edentata) – including 14 species of Armadillos (Dasypodidae) – Chiroptera, Cervidae and Rodentia – especially the hystricognaths and caviomorphs. The

authors also deal with the Cetacea that live close to the Atlantic and Pacific shores of the continent.

All data are presented very clearly and in considerable detail. It is natural that a book compiling and presenting such a large amount of information from very different sources, also includes small inconsistencies: on page 236 the scientific name of the Vicuna is *Vicugna vicugna,* on plate 13, however, one finds *Lama vicugna* and, finally, in the index of scientific names on page 428 *Vicugna (Lama) vicugna.*

P. Langer, Gießen

Heinrich, D.: **Untersuchungen an Skelettresten wildlebender Säugetiere aus dem mittelalterlichen Schleswig – Ausgrabung Schild 1971–1975.** Ausgrabungen in Schleswig. Berichte und Studien 9. Neumünster: Karl Wachholtz Verlag 1991. 204 S., 38 Abb., 106 Tab. Brosch. DM 70,–. ISBN 3-529-0145

Die vorliegende Bearbeitung der wildlebenden Säugetiere aus den Ausgrabungen des mittelalterlichen Schleswig ergänzt die in der gleichen Reihe schon publizierten der domestizierten Säuger. Mit 21 bestimmbaren Arten machten Wildsäuger mit 1350 Knochen(fragmenten) nur 1,2 % aller in diesen Grabungen gefundenen Säuger-Reste aus. Den weit überwiegenden Anteil aller Wildsäuger stellen Reh, Rothirsch, Feldhase, Rotfuchs und Wildschwein. Für die wesentlichen Arten werden in gleicher Weise Fragmentierungsgrad, Erhaltungszustand, Häufigkeit der Skelettelemente, Zerlegungsspuren, Alter, Geschlechterverhältnis, Körpergröße und Gestalt, Besonderheiten, zoogeographisch-ökologische und kulturgeschichtlich-ökonomische Aspekte abgehandelt. Die mit weniger Material belegten Arten werden entsprechend kürzer diskutiert, aber auch hier alle relevanten Gesichtspunkte dieses Kataloges. Bemerkenswerte Funde sind Knochen(fragmente) von Walroß, Pottwal, 3 Dhociden-Arten sowie die frühesten Nachweise von Damhirsch und Kaninchen für den Raum.

Dies ist eine sehr sorgfältige und umfassend dokumentierte Bearbeitung, deren Publikation in der vorliegenden ansprechenden Form die Deutsche Forschungsgemeinschaft unterstützte. Der Autor stellt seine Befunde aus den Grabungen in Schleswig in einen größeren zeitlichen und räumlichen Zusammenhang und ist in seiner Deutung der Funde sehr ausgewogen. Für einige Arten erlaubt die Auswertung des Fundmaterials einen Größenvergleich zwischen mittelalterlichen und rezenten Vertretern der Art in Schleswig-Holstein, ebenso sind begrenzt Rückschlüsse auf ihre relative Häufigkeit in der Umgebung Schleswigs im Mittelalter möglich.

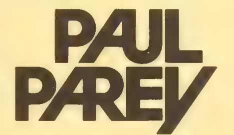
Diese Analyse belegt exemplarisch, welche weitreichenden Aufschlüsse bei sorgfältiger Arbeitsweise und entsprechender Fundortsituation mit Hilfe der Archäozoologie in zoologischer und kulturgeschichtlicher Hinsicht zu gewinnen sind. Nicht zuletzt wird auch deutlich, daß derartige Bearbeitungen nur auf der Grundlage umfangreicher und sorgfältig dokumentierter Vergleichssammlungen rezenten Materials möglich sind. Über den engeren Kreis der archäozoologischen und säugetierkundlichen Interessenten hinaus darf man dieses Buch durchaus auch ernsthaft kulturgeschichtlich Interessierten einmal als Lektüre empfehlen, um ihnen eine Vorstellung von den Methoden und der Aussagefähigkeit archäozoologischer Untersuchungen zu vermitteln.

G. Peters, Bonn

Jones, Jr., J. K.; Manning, R. W.: **Illustrated key to skulls of genera of North American land mammals.** Lubbock, Texas: Texas Tech University Press 1992. III + 75 pp., 49 figs. US $ 9.95. ISBN 0-89672-289-9

The identification and classification of mammals is heavily based on characters of the skull and the dentition, and a serious student of mammalogy will soon come across the problem of telling skulls and teeth apart. What he or she will need in that case is either a comprehensive mammal collection or a booklet like the one written by Jones and Manning. It covers 28 families of North American land mammals and figures many of the genera in photographs or line drawings. Dichotomous keys are provided to identify the order, family, and genus of a given skull. A glossary explains technical terms and the nomenclature of bones, processi and foramina of mammal skulls and the cusps and crests of teeth. The quality of the photographs is excellent, however, for esthetical reasons it is regrettable that the publisher did not invest the time and money to cast the black background of the photographic plates. In general, this is an exellent aid for the identification of skulls of North American mammals. The authors should be encouraged to continue their work and to prepare a similar key to the skulls of land mammals of Mexico and Central America.

R. Hutterer, Bonn



Erscheinungsweise und Bezugspreis 1993: 6 Hefte bilden einen Band. Jahresabonnement Inland: DM 378,– zuzüglich DM 13,80 Versandkosten; Jahresabonnement Österreich: öS 2940,– zuzüglich öS 140,– Versandkosten; Jahresabonnement Schweiz: sfr 364,– zuzüglich sfr 17,50 Versandkosten; Jahresabonnement EG-Binnenmarkt-Länder mit USt-ID-Nr.: DM 354,– zuzüglich DM 16,82 Versandkosten; Jahresabonnement EG-Binnenmarkt-Länder ohne USt-ID-Nr. und Drittländer: DM 378,– zuzüglich DM 18,– Versandkosten. Das Abonnement wird zum Jahresanfang berechnet und zur Zahlung fällig. Es verlängert sich stillschweigend, wenn nicht spätestens am 15. November eine Abbestellung im Verlag vorliegt. Die Zeitschrift kann bei jeder Buchhandlung oder bei der Verlagsbuchhandlung Paul Parey, Spitalerstraße 12, W-20095 Hamburg, Bundesrepublik Deutschland, bestellt werden. Die Mitglieder der „Deutschen Gesellschaft für Säugetierkunde" erhalten die Zeitschrift unberechnet im Rahmen des Mitgliedsbeitrages.

Z. Säugetierkunde 58 (1993) 3, 129–200

...4), 201–256, August 1993 ISSN 0044-3468 C 21274 F

ZEITSCHRIFT FÜR SÄUGETIERKUNDE

INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Organ der Deutschen Gesellschaft für Säugetierkunde





Verlag Paul Parey Hamburg und Berlin

This journal is covered by Biosciences Information Service of Biological Abstracts, and by Current Contents (Series Agriculture, Biology, and Environmental Sciences) of Institute for Scientific Information

---

Die Zeitschrift für Säugetierkunde veröffentlicht Originalarbeiten und wissenschaftliche Kurzmitteilungen aus dem Gesamtgebiet der Säugetierkunde, Besprechungen der wichtigsten internationalen Literatur sowie die Bekanntmachungen der Deutschen Gesellschaft für Säugetierkunde. Verantwortlicher Schriftleiter im Sinne des Hamburgischen Pressegesetzes ist Prof. Dr. Dieter Kruska.

Zusätzlich erscheint einmal im Jahr ein Heft mit den Abstracts der Vorträge, die auf der jeweiligen Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde gehalten werden. Sie werden als Supplement dem betreffenden Jahrgang der Zeitschrift zugeordnet. Verantwortlich für ihren Inhalt sind ausschließlich die Autoren der Abstracts.

Manuskripte: Manuskriptsendungen sind zu richten an die Schriftleitung, z. Hd. Prof. Dr. Dieter Kruska, Institut für Haustierkunde, Biologiezentrum der Christian-Albrechts-Universität, Am Botanischen Garten 9, D-24118 Kiel, Bundesrepublik Deutschland. Für die Publikation vorgesehene Manuskripte sollen gemäß den „Redaktionellen Richtlinien" abgefaßt werden. In ihnen finden sich weitere Hinweise zur Annahme von Manuskripten, Bedingungen für die Veröffentlichung und die Drucklegung, ferner Richtlinien für die Abfassung eines Abstracts und eine Korrekturzeichentabelle. Die Richtlinien sind auf Anfrage bei der Schriftleitung und dem Verlag erhältlich.

Sonderdrucke: Anstelle einer Unkostenvergütung erhalten die Verfasser von Originalbeiträgen und Wissenschaftlichen Kurzmitteilungen 50 unberechnete Sonderdrucke. Mehrbedarf steht gegen Berechnung zur Verfügung, jedoch muß die Bestellung spätestens mit der Rücksendung der Korrekturfahnen erfolgen.

Fortsetzung 3. Umschlagseite

 Verlag: Paul Parey GmbH & Co. KG, Hamburg und Berlin. Anschriften: Spitalerstr. 12, D-20095 Hamburg; Seelbuschring 9–17, D-12105 Berlin, Bundesrepublik Deutschland. – Printed in Germany by Westholsteinische Verlagsdruckerei Boyens & Co., Heide/Holst.

Z. Säugetierkunde 58 (1993) 201–211

ISSN 0044-3468

On the behaviour and social organisation of Agile wallabies, *Macropus agilis* (Gould, 1842) in two habitats of northern Australia

By W. Dressen

Lehrstuhl für Verhaltensphysiologie, Fakultät für Biologie, Universität Bielefeld, Germany

Receipt of Ms. 3. 8. 1992
Acceptance of Ms. 26. 2. 1993

Abstract

The behaviour, population characteristics and patterns of association of the agile wallaby *Macropus agilis* were recorded over five months during the dry and late dry season in two habitats at Kapalga, Northern Territory, Australia. Mean population density of wallabies in a monsoon forest was estimated to be approximately 6.5 times greater than in open eucalypt woodland. In both populations, the sex ratio of adult animals was significantly biased towards females. The mean size of associations was higher in the monsoon forest. Larger associations in both habitats were temporary and represented aggregations at spatially concentrated resources: foraging areas, water and shelter sites. Females with their independent offspring and small males were essentially solitary. Large and medium-sized males were always seen associated with females of different size classes. Gregariousness in *M. agilis* was correlated with population density which appeared to depend on the habitat and the distribution and availability of food. The solitariness of young males and stability of female groups in the eucalypt woodland may be a result of females remaining within the home range of their mothers whereas young males may separate and disperse soon after weaning.

Introduction

The sandy or agile wallaby *Macropus agilis* (Gould, 1842) is the most common macropodid of the northern tropical region of Australia inhabiting open savanna woodland as well as more dense riverine and monsoon forests with adjacent grasslands (Bolton 1974; Merchant 1983). Like other larger macropodids, the species is dimorphic, and males reach sizes between 20–30 kg, about double the size of females (Merchant 1983; Newsome 1983). In spite of its abundance, surprisingly little is known about its social organisation and ecology. Johnson (1980) analysed group composition of *M. agilis* in North Queensland not knowing identities of individuals. He found single animals as the most commonly observed social unit and suggested that "in the small groups the most frequent relationship appeared to be the sexual assocation between female and male; in the larger groups feeding seemed to be the basis of association ...". In his socio-ecological study on three sympatric macropodid species in the Northern Territory, Croft (1987) likewise concluded that *M. agilis* is essentially solitary.

This study presents results of a five months investigation on two populations of agile wallabies in the wet-dry tropics of Northern Australia. Here, the availability of resources fluctuates greatly each year, resources become limited and clumped in the late dry season, and abundant but spread out during and following the wet season (Ridpath 1985). The study was conducted during the dry and late dry season in two habitats with obvious differences in the availability of water and food. The objective of the study was to describe the behaviour of individuals and of associations, and to compare the population characteristics at both sites. Furthermore, the analysis of the composition and stability of

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5804-0201 $ 02.50/0

associations with known individuals should reveal how ecological factors influence the spatial and social organisation of agile wallabies.

Material and methods

Study site

The study was conducted at Kapalga Research Station (132° 25′ E, 12° 37′ S) in Kakadu National Park, Northern Territory, Australia. The region has a marked monsoonal climate with two distinct seasons, the "wet" and the "dry". Whereas temperatures are always high and daylength varies little, the mean annual rainfall of 1100–1600 mm is strongly seasonal spread mainly over 4–5 months from November to March (McAlpine 1976; Nix 1981). June to September is a period of intense drought whilst April to May and October to November are transitional. Two different habitats were chosen: 1. open eucalypt woodland with the dominant tree species *Eucalyptus miniata* and *E. tetradonta*; 2. a pocket of lowland monsoon forest (about 1 km^2) adjacent to seasonally flooded sedgelands on one side and eucalypt woodland on the other.

Collecting data

Observations were made over 5 months from July to November, 1991. They were made from fixed observation sites and from four transect lines. Data were collected principally on general activity, features of individual animals, social behaviour, size and composition of associations and groups, and food items. Both areas were extensively traversed on foot (210 field hours) to record activity and movement patterns of selected individuals and to collect data on composition of and changes in associations of wallabies. Continuous observation was conducted when the wallabies tolerated the observer's presence and continued until the wallabies moved out of sight. Within the monsoon forest animals were often disturbed by the observer and occasionally responded with foot-thumps and fleeing; usually however they moved only short distances (< 50 m) to nearby dense vegetation. Wallabies in the eucalypt woodland site had larger fleeing distances (> 100 m) and it was difficult to follow them on foot.

Behavioural data were also collected from fixed observation sites (130 observation hours) and spotlighting (18 hours). Information on social interactions were collected by all-occurrences samples (Altmann 1974) within one-minute intervals. 102.5 hours of these behavioural observations with a protocol (monsoon forest: 54.5; eucalypt woodland: 48 hours) were evaluated. Frequency of a behaviour was calculated per hour, and interaction rates represent the number of interactions per hour when an animal was in association with one or more wallabies.

Activity budgets were calculated from six 12-hour daytime observations in October and November. The percentage of time spent by all animals in each category of activity was calculated for each hour.

Estimating density

Estimates of population density were based on 24 replicated transect counts. Density was estimated from individuals seen within a predefined distance up to 100 m (depending on sightability within a micro-habitat) either side of two transect-lines (strip-transect method, cf. Southwell 1989) within each habitat. The transect-lines (one km each) were checked on at least three days per month between 7.00–9.00 h and 16.00–18.00 h. In the open woodland site one transect-line was adjacent to a billabong, the other was 2.0 km away from that billabong. In the monsoon forest site, one transect was within the transition zone between the monsoon forest and the eucalypt woodland, the other was within the monsoon forest.

Size and sex classification

The animals were separated by sex and size into 7 classes: large males (Ml; males significantly larger than females, partly heavily muscled on forearms and shoulders; > 15 kg), medium males (Mm; males of same size as adult females; about 8–15 kg), small males (Ms; less than 8 kg), large females (Fl; about > 12 kg), medium females (Fm; about 8–12 kg), small females (Fs; less than 8 kg) and young-at-foot (of either sex). Estimated weights were verified by known size/weight relations from captive animals. Females (Fl and Fm) were further subdivided into those without pouch young (F), with small (Fp) or large pouch young (Fpy; head often out of pouch) and those who were accompanied by a young-at-foot (Fyaf). For analysis F, Fp and Fpy were pooled, and Fyaf was treated as a single unit unless otherwise stated.

Identifying individuals

Many individuals could be identified on the basis of the shape, number and location of ear notches and black spots on the ears. However these markings could only be reliably recognised at distances up to 80 m using a 10×40 binoculars. Mature females were easily recognized by natural ear markings. Other individual external features included a missing tonus of the tail (during hopping), a blind/missing eye, and distinctive face scars. Individual variations in the colour of the fur were less conspicuous. The white facial stripe – as used for individual recognition in the whiptail wallaby, *Macropus parryi* (Kaufmann 1974) – was not a useful distinguishing feature in *M. agilis* because of its uniform shape. In total 16 male and 28 female wallabies could be identified using external features.

Definitions of groupings

Two individuals were assumed to be associating when within about 50 m of each other. A group was defined as an association of individuals resting and moving close together with attentiveness for and orientation to the behaviour of the other group member(s) resulting in coordinated movement patterns. The lability of an association was defined as the number of wallabies joining or leaving a grouping during a 30 min observation bout divided by the number of animals at the beginning of the observation bout (Johnson 1989b). Average values of this lability index ("group flux") were calculated for five size/sex classes of single and associated foraging animals (single; female with young-at-foot; single sex association $N = 2$, and $N \geq 3$; mixed sex association $N = 2$, and $N \geq 3$).

Results

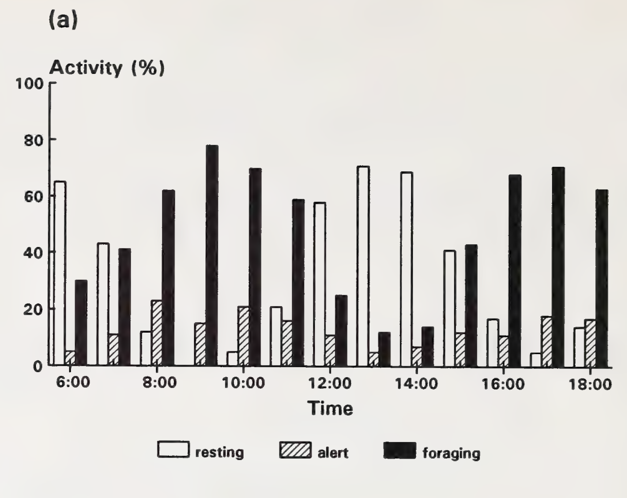
Habitat utilization

In the monsoon forest wallabies rested during daylight hours between buttresses of large trees, in shallow depressions which they scraped or beneath fallen logs and dense vegetation. Wallabies were active during mornings and afternoons when they moved between 0.6 and 1.5 km (N = 12) from their resting sites. They dispersed within the forest digging for roots and foraging for fallen fruits mainly *Ficus racemosa, Carpenteria* sp. and flowers and green fruits of the Kapoktree (*Bombax ceiba*). Between 19.30 and 21.00 h between 2 and 12 wallabies (mean: 5.3, N = 12 counts) were seen grazing on the grassy floodplains adjacent to the monsoon forest. When spotlighted they immediately escaped to the forest.

In July and August (dry season) wallabies in the eucalypt woodland grazed close to billabongs only during the night and moved daily to the billabong from non-adjacent areas ($>$ 0.5 km). From September to October (late dry season) wallabies shifted their main activity centres closer to the billabong. They were observed drinking and grazing on the open areas close to the remaining water during morning and late afternoon hours (Fig. 1). They spent the hottest part of the day in the adjacent woodland resting usually under tussocks of grass.

Patterns of activity

During the day wallabies in the monsoon forest site were more active, especially in foraging, than wallabies in the eucalypt woodland (Fig. 1), and they rested predominantly between 12.00 and 15.00 h compared to 11.00–17.00 h for the eucalypt woodland population. Activity bouts for the eucalypt woodland wallabies were from 7.00–10.00 h and from 16.00 h on. During these periods most wallabies drank once every day, others were observed drinking every second day. As the dry season progressed, the water level of the billabong rapidly receded. This provided the major source of green grasses and forbs for wallabies in both day and night feeding sessions. After arriving at the billabong wallabies spent 4.1 ± 2.4 min (N = 48) drinking followed by 38 ± 14.6 min (N = 48) grazing close to the water. When grazing on this open area, wallabies spent more time exhibiting alert behaviour than wallabies which foraged in the monsoon forest.



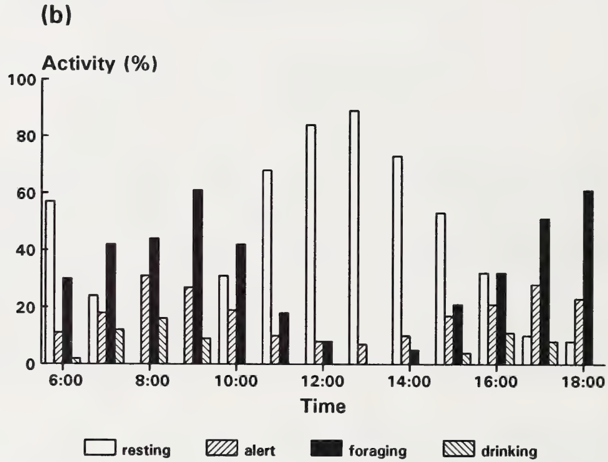


Fig. 1. Activity budget of *Macropus agilis* in monsoon forest (a) and in eucalypt woodland (b)

Density and sex ratio

Table 1 shows the mean density of wallabies calculated for both habitats from 24 transect counts. If both seasons and transect lines per habitat are combined the mean density at the monsoon forest population was approximetely 6.5 times larger than the eucalypt woodland population. The increase in density in the woodland between early and late dry season was probably due to wallabies congregating on areas with permanent water. The density in the monsoon forest remained stable throughout. Density was lower at line 2 placed in the transition zone adjacent to the eucalypt woodland.

At both study sites the overall sex ratio (male : female) was significantly biased towards females. In the open woodland sex ratio was 0.535 ($N = 109$, $\chi^2 = 9.99$, $P < 0.01$), in the monsoon forest sex ratio was 0.57 ($N = 168$, $\chi^2 = 12.59$, $P < 0.01$). Sex ratio disparity was most pronounced in medium and large size classes, whereas sex ratio in the small size class was not significantly different from 1.0 (Tab. 2). These data suggest that there was a trend of bias of sex ratio towards females with increasing age.

Table 1. **Mean densities (± SD) of *Macropus agilis* (km^{-2}) observed during dry and late dry season in two habitats**

Habitat		Dry season		Late dry season	
Eucalypt woodland	line 1	7.12	± 5.74	16.67	± 9.23
	line 2	2.78	± 3.28	1.67	± 2.89
Monsoon forest	line 1	61.67	±19.08	58.33	±25.76
	line 2	31.6	±16.75	30.83	±17.54

Table 2. **Sex ratio (male : female) of *Macropus agilis* in two habitats**

Habitat	Size class	Males	Females	Sex ratio	χ^2	P
Eucalypt woodland	large	8	22	0.364	6.53	<0.01
	medium	19	43	0.442	9.29	<0.01
	small	11	6	1.833	1.47	>0.225
Monsoon forest	large	15	50	0.30	18.85	<0.001
	medium	19	35	0.543	4.74	<0.05
	small	27	22	1.227	0.51	>0.475

P: significance of difference from a 1:1 ratio (χ^2-Test).

Social behaviour

Agile wallabies interacted with conspecifics at a rate of 0.85 interactions per hour (N = 91.5 hours of observation of associated wallabies excluding consort interactions). There were 44 (56.4 %) agonistic, and 26 (33.3 %) sexual and 8 (10.3 %) other non-agonistic interactions.

The most frequent agonistic interaction (0.37 h^{-1}) was the approach-retreat-encounter (N = 34; 43.6 %): one animal approached a conspecific which retreated after short mutual sniffing (N = 14; 17.9 %) or without a sniffing contact (N = 20; 25.6 %). Members of all age/sex classes could be involved in this type of agonistic interaction. Those sequences preceded by a naso-nasal or naso-body contact often involved biting, grabbing and/or kicking by one animal whereas the other usually crouched and jumped away.

The most distinctive agonistic behaviour was standing on tip-toes with a crouched body posture using the tail as a prop (Fig. 2). The body position resembles that of the "stiff-legged walk" described for other macropodids (cf. Kaufmann 1974; Coulson 1989) except that the opponents did not walk but stood motionless for several seconds in frontal or broadside position with their head lowered. This behaviour was shown in agonistic encounters between and within both sexes. It was performed by either or both interacting animals and resulted in the retreat of one animal (N = 6) or exaggerated grooming followed by grazing of both opponents (N = 2). Fights were rarely seen (N = 2) and were characterized by grappling and sparring between both opponents. Both fights were performed by Ms-males with no obvious winner. Stereotyped agonistic displays described for large macropodids (cf. Ganslosser 1989) were not seen in the field. In captivity, grass-pulling combined with standing-high and rubbing of grass and branches against the chest has been observed in male agile wallabies following agonistic encounters.

Observations of anoestrous sexual interactions (N = 26; 33.3 %; 0.28 h^{-1}) were similar to that of other macropodids: while the male pawed a female's tail he had a partly or fully erected penis and simultaneously lashed his tail, and nosed the female's cloaca. This "sexual checking" (Kaufmann 1974) usually caused the female to retreat but occasionally elicited urination. Nosing of the cloaca was also observed twice between males. In both encounters

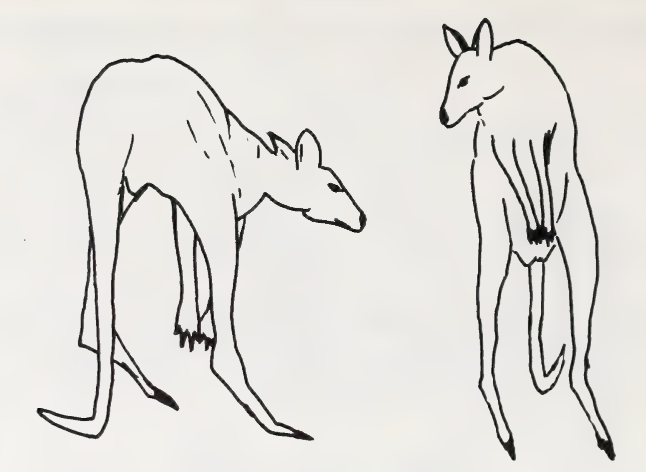


Fig. 2. Standing on tip-toes in broadside position during an agonistic encounter between two male agile wallabies

Ms was 'checked' by Mm; the younger male hissed and struck with his paws against the older before retreating.

Patterns of association

Females who were obviously approaching oestrus were persistently followed by 1–4 males. One large male (Ml) tended to follow the oestrous female continually whereas smaller males (Mm and/or Ms) remained within 20 m. Within these consort-groups sexual behaviour patterns resembled those of non-oestrous sexual interactions but male sexual behaviour was more frequent and vigorous. In 9 consort-groups females interacted with the consorting males at 2.82 interactions per hour (N = 8.5 hours of observation). Sexual behaviour of the smaller males was often interrupted by the approach of the largest and dominant male. No successful mounting and copulation was observed (N = 4 attempts). Data on duration and consistency of members within a consort-group were not collected because wallabies were too mobile to allow the collection of regular and continuous data.

The frequencies of associations for various size/sex classes performing foraging and resting behaviour are shown in table 3. In the monsoon forest the mean frequency of association were higher (foraging: 2.51, resting: 2.45 versus 2.21 and 1.62 respectively in the eucalypt woodland). Foraging and resting wallabies were more solitary in the eucalypt woodland than wallabies in the monsoon forest (19.6 and 30.4 % versus 10.7 % and 12.2 % respectively). Wallabies observed alone at the beginning of a 30 min observation bout remained so in 80 % of cases in the monsoon forest (N = 60 bouts) and in 86 % of bouts in the eucalypt woodland (N = 51) (Tab. 4).

Adult females with young-at-foot were recorded alone more frequently than other associations (Tab. 3). They occasionally associated with other wallabies when feeding but rarely did so when resting. Large and medium sized males were usually associated with mixed sex associations whereas small males were essentially solitary. Apart from the mother-young group, the most permanent association was between females in the eucalypt woodland. Four female pairs and one female trio were observed over 35–77 days (mean: 50.2 days). Most of these females were of different size-classes. Group members rested close together and were strongly cohesive when associated with other wallabies. Cohesive groups were most conspicuous during the late dry season when larger aggregations of wallabies were grazing and drinking at the billabong. Groups arrived and left this area with

Table 3. **Types of association and frequency (%) of each size/sex class in the late dry season**

Habitat	Activity	Association	Size/sex class Ml	Mm	Ms	Fl	Fm	Fs	Fyaf
Eucalypt woodland	foraging	single	8.3	22.6	43.8	20.5	21.4	20.0	58.3
		single sex N = 2	16.7	3.2	6.2	17.9	16.7	13.3	–
		single sex N ≧ 3	8.3	3.2	6.2	7.7	9.5	13.3	16.7
		mixed sex N = 2	0	22.6	12.5	5.1	14.3	6.7	–
		mixed sex N ≧ 3	66.7	48.4	31.3	48.7	38.1	46.7	25.0
		No. indiv.	12	31	16	39	42	15	12 × 2
	resting	single	11.1	26.1	75.0	33.3	32.3	42.8	100
		single sex N = 2	11.1	13.0	0	29.6	22.6	14.3	–
		single sex N ≧ 3	0	0	0	3.7	6.4	0	0
		mixed sex N = 2	33.3	43.5	12.5	22.2	22.6	14.3	–
		mixed sex N ≧ 3	44.4	17.4	12.5	11.1	16.1	28.6	–
		No. indiv.	9	23	8	27	31	7	5 × 2
Monsoon forest	foraging	single	0	0	17.2	18.7	13.5	16.0	32.0
		single sex N = 2	0	0	10.3	6.3	10.8	4.0	–
		single sex N ≧ 3	0	14.3	10.3	16.7	16.2	16.0	28.0
		mixed sex N = 2	0	9.5	20.7	6.3	10.8	4.0	–
		mixed sex N ≧ 3	100	76.2	41.4	52.0	48.6	60.0	40.0
		No. indiv.	14	21	29	48	37	25	25 × 2
	resting	single	10.5	8.0	34.8	9.3	8.6	26.9	80.9
		single sex N = 2	5.3	4.0	8.7	11.6	11.4	11.5	–
		single sex N ≧ 3	0	0	0	7.0	17.1	15.4	0
		mixed sex N = 2	5.3	8.0	4.3	7.0	2.9	0	–
		mixed sex N ≧ 3	78.9	80.0	52.2	65.1	60.0	46.2	19.1
		No. indiv.	19	25	23	43	35	26	21 × 2

coordinated movements over the open grassy bed. Other individuals rarely joined in although some males temporary accompanied female groups. Next to the mother-young group, female pairs had the lowest lability index (Tab. 4). The mean change in composition per observation bout was 0.22 in monsoon forest (N = 31 bouts) and 0.08 in eucalypt woodland (N = 24).

In both habitats mixed sex associations (N ≥ 3 wallabies) were the most frequent type of association during foraging. These associations were not persistent through time as indicated by the highest lability indices (Tab. 4). The mean change in composition of mixed sex associations was 0.96 in monsoon forest (N = 22 bouts) and 1.31 in eucalypt woodland (N = 29).

Table 4. **Mean lability index of associations for foraging wallabies in two habitats**

Association	Monsoon forest			Eucalypt woodland		
	N_a	N_b	Index	N_a	N_b	Index
Single	23	60	0.2	35	51	0.14
Fyaf	8	22	0.07	7	25	0
Single sex N = 2	6	31	0.11	10	24	0.04
Single sex N ≧ 3	7	22	0.15	3	8	0.16
Mixed sex N = 2	8	28	0.1	9	21	0.11
Mixed sex N ≧ 3	18	54	0.23	17	29	0.25

N_a: No. of associations, N_b: No. of observation bouts.

Discussion

In the tropical lowlands of the Northern Territory of Australia, the agile wallaby *Macropus agilis*, occurs in various habitats with evident differences in population density. The widespread occurrence may be due to its general adaptability as a grazer and browser, and to its high fecundity compared with other tropical macropodids. Given its capability for continuous breeding (Kirkpatrick and Johnson 1969; Merchant 1976) and the early sexual maturity of females at about 10–12 months of age (Merchant 1976), rapid population growth might be expected under favourable conditions. Despite the markedly seasonal climate, over 90 % of all adult females examined by Bolton et al. (1982) were fully reproductive. At Kapalga, *M. agilis* is the most common macropodid in both habitats under study with low densities in the major habitat, the eucalypt woodland, and higher densities in the monsoon forest. The only other macropodid species present at the Kapalga area is the antilopine wallaroo *Macropus antilopinus*. This species is much less common in the open woodland and has never been observed at the monsoon forest site (Corbett, pers. comm.). Monsoon forests are small restricted and isolated and are regarded as the most important fructivorous plant community of the Kakadu National Park region producing fleshy fruits and nectar all year round (Taylor and Dunlop 1985). During the dry season the density of wallabies in the monsoon forest remained stable although free water was not available from the end of August until January. Wallabies in the monsoon forests were sedentary and presumably obtained their water requirements from fruits and roots. In contrast wallabies in the eucalypt woodland responded to seasonal availability of food and water by moving to permanent waters and associated green food supplies.

At both study sites adult females outnumbered males. This sex ratio has also been described for populations of other macropodids such as the whiptail wallaby, *Macropus parryi* (Kaufmann 1974), the red kangaroo, *M. rufus* (Newsome 1977; Johnson and Bayliss 1981), the eastern grey kangaroo, *M. giganteus* (Jarman and Southwell 1986) and the western grey kangaroo, *M. fuliginosus* (Norbury et al. 1988; Arnold et al. 1991) along with several explanatory hypotheses. Johnson and Bayliss (1981) attributed the skewed ratio in a population of *M. rufus* to a higher mortality in males resulting possibly from dispersal into suboptimal habitats. Norbury et al. (1988) argued that sexual dimorphism in body weight may impose higher nutritional demands for males which can be critically during periods of food shortage. A biased sex ratio might also result from different juvenile mortality in the sexes. Russell (1982) showed that in marsupials heaviest mortality tend to fall after pouch life has been completed. In *M. rufogriseus*, for instance,

mortality was highest during the period when infants were still suckling from their mothers following them as young-at-foot (Johnson 1989a). The high mortality was attributed to the competition between females limiting their ability to sustain higher levels of lactation during late pouch life and early life out of pouch.

Reasons for the female-biased sex ratio of adult *M. agilis* are not obvious. Intrasexual competition in females may operate on a seasonal base, for example during the dry season when resources become limited and clumped, but also during the wet season in areas where dry season feeding grounds are flooded (cf. Bolton et al. 1982). Furthermore, predation by dingoes, *Canis familiaris dingo*, may be a significant factor in juvenile mortality. At Kapalga, dingoes focus on seasonally available magpie geese, *Anseranas semipalmata* and dusky rats, *Rattus colletti*, but wallabies are the most consistent eaten prey throughout the year (Corbett 1989) and predominate in those wet seasons when rat numbers are low (Corbett pers. comm.). Solitariness of subadult male agiles suggests that sons separate earlier from their mothers than daughters of similar age. It is possible that by separation and dispersal into less suitable habitats, young males are exposed to greater dingo predation than young females.

Previous studies suggested that *M. agilis* is essentially solitary, its mean group size being close to unity (Johnson 1980; Croft 1987). However, in Johnson's (1980) study more individuals were counted in association with other wallabies ($N \geq 478$) than those seen alone ($N = 395$). Field studies conducted on different macropodid species analysed group size and composition which were regarded as an index of sociality and dispersion. Studies on *M. rufus* (Newsome 1965), eastern wallaroos, *M. r. robustus* (Taylor 1982), *M. giganteus* (Taylor 1982; Southwell 1984a) and *M. fuliginosus* (Johnson 1983) demonstrated a relationship between mean group size and population density, whereas Johnson (1989b) showed for *M. rufogriseus* that average group size varied seasonally, but was not influenced by population density. The different degree of gregariousness may therefore be a result of different population density rather than a truely social phenomenon especially when arbitrary defined distances between animals are used to denote a number of individually unknown animals as a group.

The results of this study indicate that the size of associations in *M. agilis* is also related to population density. During the dry and late dry season the mean size of associations was higher in the monsoon forest where wallaby density was greatest. Animals of different size/sex classes differed in the extent to which they were found alone or in association with other individuals. As in other macropodids, females with young-at-foot were the most solitary class (e.g. Taylor 1982; Jarman and Southwell 1986). Small males were essentially solitary whereas large and medium sized males were always seen with a female or in larger mixed sex associations. This contrasts to macropodid species such as *M. rufus* and *M. giganteus* where large males were seen alone more often than other male classes (Croft 1981b; Jarman and Southwell 1986). This is believed to be due to their high mobility in search for oestrous females, and might therefore depend on the female breeding pattern. Males of the larger kangaroo species form transient rather than long-term consort-relationships with females approaching oestrus and a size-based dominance-hierarchy among males is regarded as determining final priority of access to oestrous females (Russell 1984).

Larger associations in *M. agilis* lasted only for several hours and probably represented coincidental aggregations around a spatially concentrated resource such as water, fruiting trees, green grass, and shelter sites. Associations resembled those described for the gregarious macropodids with an unstable composition containing varying combinations of animals of all ages and both sexes (Russell 1984; Jarman and Coulson 1989). The duration of consort-groups, recognized by the high amount of sexual behaviour of males, could not be assessed because of the high mobility of these groups (cf. Jarman and Southwell 1986). In the woodland a high proportion of female groups could be observed.

They were characterized not only by small distances between individuals but also by their persistence over time, by a cohesive and coordinated movement pattern and by the orientation of each member to the behaviour of other members. They might derive from mother-offspring units when daughters settle within their mothers' home range whilst sons disperse soon after weaning as described for *M. rufogriseus* (JOHNSON 1986). However, given the short duration of this study, it is not known how associations may change in the wet season and whether or not female groups are permanent social units. Moreover, factors that favour female group formation at low population density remain to be determined.

Acknowledgements

The work was conducted while I held a postgraduate research scholarship from Deutscher Akademischer Austauschdienst, Bonn. This scholarship and additional financial assistance from the Westfälisch-Lippische Universitätsgesellschaft, Bielefeld, is gratefully acknowledged. I am especially grateful to L. CORBETT, CSIRO Darwin, for his help and encouragement during this study. L. CORBETT and E. RUSSELL made valuable comments and improvements on the manuscript, H. HENDRICHS, Universität Bielefeld, supported the study in Germany. I like to thank the staff of CSIRO Darwin, Division of Wildlife and Ecology, for assistance, especially M. DOUGLAS, R. EAGER, M. GILL and T. HERTOG. Finally I thank A. PRESS, Australian National Parks and Wildlife Service, for the permit to conduct research in the Kakadu National Park.

Zusammenfassung

Beobachtungen zum Verhalten und zur sozialen Organisation des Flink-Wallabys, Macropus agilis (Gould, 1842), in zwei Habitaten Nordaustraliens

Es wurden Verhalten, Zusammensetzung und Stabilität der Verbände sowie Populationsmerkmale des Flink-Wallabys in zwei Habitaten Nordaustraliens – Monsunwald und Eukalyptussavanne – untersucht. Die Beobachtungen fanden über fünf Monate während der Trockenzeit im australischen Kapalga, Nord-Territorium, statt. Die Populationsdichte im Monsunwald war durchschnittlich 6,5 mal höher als die in der Eukalyptussavanne. In beiden Populationen war das Geschlechterverhältnis der Adulttiere signifikant in Richtung der Weibchen verschoben. Größere gemischtgeschlechtliche Verbände waren nicht dauerhaft und stellten Aggregationen an lokal begrenzten Ressourcen wie Wasserstellen, Weide- und schattigen Ruheplätzen dar. Ihre Größe korrelierte mit der Populationsdichte, die vom Habitat sowie der Verteilung und Verfügbarkeit der Nahrung abhängig zu sein scheint. Während mittelgroße und große Männchen überwiegend mit Weibchen verschiedener Größenklassen assoziiert waren, zeigten junge Männchen sowie Weibchen mit noch nicht entwöhntem Jungtier deutliche Tendenzen zu solitärer Lebensweise. Die beschriebenen sozialen Strukturen und Populationsmerkmale werden mit denen anderer bisher untersuchter Känguruharten verglichen. Die solitäre Lebensweise junger Männchen und die beobachteten stabilen Weibchen-Einheiten entstehen vermutlich durch den Verbleib weiblicher Nachkommen bei der Mutter, während die männlichen Nachkommen sich früh nach der Entwöhnung vom Muttertier trennen.

References

ALTMANN, J. (1974): Observational study of behavior: sampling methods. Behaviour **49**, 227–267.

ARNOLD, G. W.; GRASSIA, A.; STEVEN, D. E.; WEELDENBURG, J. R. (1991): Population ecology of western grey kangaroos in a remnant of wandoo woodland at Baker's Hill, southern Western Australia. Wildl. Res. **18**, 561–575.

BOLTON, B. L. (1974): An ecological study of the agile wallaby on the coastal plains of the Northern Territory with a comparison between improved and unimproved areas. MVSc thesis, Univ. Queensland, Brisbane.

BOLTON, B. L.; NEWSOME, A. E.; MERCHANT, J. C. (1982): Reproduction in the agile wallaby *Macropus agilis* (Gould) in the tropical lowlands of the Northern Territory: opportunism in a seasonal environment. Aust. J. Ecol. **7**, 261–277.

CORBETT, L. K. (1989): Assessing the diet of dingoes from feces: a comparison of 3 methods. J. Wildl. Manage. **53**, 2, 343–346.

CROFT, D. B. (1981a): Social behaviour of the euro, *Macropus robustus* (Gould), in the Australian arid zone. Aust. Wildl. Res. **8**, 13–49.

— (1981b): Behaviour of red kangaroos, *Macropus rufus* (Desmarest, 1822), in north-western New South Wales, Australia. Aust. Mammal. **4**, 5–58.

— (1987): Socio-Ecology of the antilopine wallaroo, *Macropus antilopinus*, in the Northern Terri-

tory, with observations on sympatric *M. robustus woodwardii* and *M. agilis*. Aust. Wildl. Res. **14**, 243–255.

Ganslosser, U. (1989): Agonistic behaviour in Macropodidoids – a review. In: Kangaroos, Wallabies and Rat-Kangaroos, Ed. by G. Grigg, P. Jarman, and I. Hume. Sydney: Surrey Beatty and Sons. Pp. 475–503.

Jarman, P. J.; Coulson, G. (1989): Dynamics and adaptiveness of grouping in macropodids. In: Kangaroos, Wallabies and Rat-Kangaroos. Ed. by G. Grigg, P. Jarman, and I. Hume. Sydney: Surrey Beatty and Sons. Pp. 527–547.

Jarman, P. J.; Southwell, C. J. (1986): Grouping, associations, and reproductive strategies in Eastern Grey Kangaroos. In: Ecological aspects of social evolution. Ed. by D. I. Rubenstein and R. W. Wrangham. Princeton, USA: Princeton University Press. Pp. 399–428.

Johnson, C. N. (1983): Variation in group size and composition in red and western grey kangaroos, *Macropus rufus* (Desmarest) and *M. fuliginosus* (Desmarest). Aust. Wildl. Res. **10**, 25–31.

— (1986): Philopatry, reproductive success of females, and maternal investment in the red-necked wallaby. Behav. Ecol. Sociobiol. **19**, 143–150.

— (1989a): Mortality of immature red-necked wallabies. J. Mammalogy **70**, 202–204.

— (1989b): Grouping and the structure of association in the red-necked wallaby. J. Mammalogy **70**, 18–26.

Johnson, C. N.; Bayliss, P. G. (1981): Habitat selection by sex, age and reproductive class in the Red Kangaroo, *Macropus rufus*, in Western New South Wales, Aust. Wildl. Res. **8**, 465–474.

Johnson, P. M. (1980): Field observations on group compositions in the agile wallaby *Macropus agilis* (Gould) (Marsupialia: Macropodidae). Aust. Wildl. Res. **7**, 327–331.

Kaufmann, J. H. (1974): Social ethology of the whiptail wallaby, *Macropus parryi*, in north eastern New South Wales. Anim. Behav. **22**, 281–369.

Kirkpatrick, T. H.; Johnson, P. M. (1969): Studies of Macropodidae in Queensland. 7. Age estimation and reproduction in the agile wallaby (*Wallabia agilis* (Gould)). Qd. J. Agric. Anim. Sci. **26**, 691–698.

McAlpine, J. R. (1976): Climate and water balance. In: Lands of the Alligator Rivers Area, Northern Territory. CSIRO Aust. Land Res. Ser. No. **38**, 35–49.

Merchant, J. C. (1976): Breeding biology of the agile wallaby *Macropus agilis* (Gould) (Marsupialia: Macropodidae) in captivity. Aust. Wildl. Res. **3**, 93–103.

— (1983): Agile Wallaby. In: Complete Book of the Australian Mammals. Ed. by R. Strahan. Sydney: Angus and Robertson. Pp. 242–243.

Newsome, A. E. (1965): The abundance of red kangaroos, *Megaleia rufa* (Desmarest), in central Australia. Aust. J. Zool. **13**, 269–287.

— (1977): Imbalance in the sex ratio and age structure of the Red kangaroo, *Macropus rufus*, in central Australia. In: The biology of marsupials. Ed. by B. Stonehouse and D. Gilmore. London: Macmillan Press. Pp. 221–233.

— (1983): The grazing Australian marsupials. In: Ecosystems of the World. 13: Tropical savannas. Ed. by F. Bourliére. Amsterdam: Elsevier. Pp. 441–461.

Nix, H. A. (1981): The environment of *Terra australis*. In: Ecological Biogeography of Australia. Ed. by A. Keast. The Hague: W. Junk. Pp. 103–133.

Norbury, G. L.; Coulson, G. M.; Walters, B. L. (1988): Aspects of the western grey kangaroo, *Macropus fuliginosus melanops*, in semi-arid north-west Victoria. Aust. Wildl. Res. **15**, 257–266.

Ridpath, M. G. (1985): Ecology in the wet-dry tropics: how different? Proc. Ecol. Soc. Aust. **13**, 3–20.

Russell, E. M. (1982): Patterns of parental care and parental investment in marsupials. Biol. Rev. **57**, 423–486.

— (1984): Social behaviour and social organisation of marsupials. Mammal. Rev. **14**, 3, 101–154.

Southwell, C. J. (1984a): Variability in grouping in the eastern grey kangaroo, *Macropus giganteus*. I. Group density and group size. Aust. Wildl. Res. **11**, 423–435.

— (1984b): Variability in grouping in the eastern grey kangaroo, *Macropus giganteus*. II. Dynamics of group formation. Aust. Wildl. Res. **11**, 437–449.

— (1989): Techniques for monitoring the abundance of kangaroo and wallaby populations. In: Kangaroos, Wallabies and Rat-Kangaroos. Ed. by G. Grigg, P. Jarman, and I. Hume. Sydney: Surrey Beatty and Sons. Pp. 659–693.

Taylor, R. J. (1982): Group size in the eastern grey kangaroo, *Macropus giganteus*, and the wallaroo, *Macropus robustus*. Aust. Wildl. Res. **9**, 229–237.

Taylor, J. A.; Dunlop, C. R. (1985): Plant communities of the wet-dry tropics of Australia: the Alligator Rivers region, Northern Territory. Proc. Ecol. Soc. Aust. **13**, 83–127.

Author's address: Dipl.-Biol. Wolfgang Dressen, Lehrstuhl für Verhaltensphysiologie, Fakultät für Biologie, Universität Bielefeld, Postfach 10 01 31, D-33501 Bielefeld, Germany

Z. Säugetierkunde 58 (1993) 212–224

ISSN 0044-3468

Pine marten (*Martes martes* Linné, 1758) comparative feeding ecology in an island and mainland population of Spain

By A. P. Clevenger

Department of Forestry, Wildlife and Fisheries, University of Tennessee, Knoxville, TN, USA

Receipt of Ms. 18. 5. 1992
Acceptance of Ms. 28. 9. 1992

Abstract

Investigated the feeding ecology of pine martens (*Martes martes*) in an insular (Minorca, Balearic Islands) and mainland (Cantabrian Mountains) Spanish population by analysis of food habits, food niche breadth, prey size index and prey weight distribution. Mammals, birds, fruits and insects were the main four dietary components in both populations. In Minorca all four were important during the year, whereas small mammals and fleshy fruits were dominant in the Cantabrian diet. The insular pine martens were characterized by having a wide food niche breadth and exploited all foods nearly equally compared to the Cantabrian martens and those from two other mainland populations. Pine marten prey size index and mean prey size also were greater in Minorca. Insular gigantism in Minorcan pine martens may be attributed to increased food abundance and reduced interspecific competition.

Introduction

Marten populations are subject to periodic food shortages, patchily distributed resources, and have been selected for a generalist feeding pattern (Erlinge 1986; Thompson and Colgan 1987). Their diets vary according to availability of different food types, their temporal variation, and degree of competition. Studies of European pine marten (*Martes martes*) diets have revealed that mammals were the most important food, whereas plant material (primarily fleshy fruits), birds, and insects were less common (Lockie 1961; Nyholm 1970; Pulliainen 1981; Moreno et al. 1988; Marchesi and Mermod 1989; Clevenger 1992).

In Spain, insular pine marten populations are found in Minorca and Majorca (Balearic Islands). Due to their geographic isolation, these environments are characterized as being depauperate in fauna compared to mainland areas (Lack 1942; Sondaar 1977; Reed 1982). Mammal prey species diversity is low and so are the number of competing small carnivores; the latter include spotted genet (*Genetta genetta*) and weasel (*Mustela nivalis*) on Majorca, whereas just the weasel is present on Minorca. Feral cats (*Felis silvestris* f. catus) are uncommon on both islands. Due to the lack of competitors and limited prey base, island pine marten would be expected to exhibit dietary differences compared to mainland populations. Distinct cranial morphology of Minorcan pine martens compared with Majorcan and those from the Iberian Peninsula (Alcover et al. 1986) suggests that the first exhibits insular gigantism and furthermore may have a unique trophic niche. In this study I describe the feeding ecology of pine marten from an insular (Minorca) and mainland Spanish population (Cantabrian Mountains), and discuss how varying levels of food resource abundance and interspecific competition may account for their divergence in body size.

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5804-0212 $ 02.50/0

Material and methods

Study area

The Balearic Island archipelago is located in the western Mediterranean approximately 150–250 km from the Iberian Peninsula and is composed of three main islands, Majorca, Minorca, and Ibiza. Minorca is the second largest island in the archipelago, covering 689 km^2 and is approximately 45 km long and 15 km wide. The highest point raises 358 m above sea level. Climate for the entire archipelago is typically Mediterranean with moderate temperatures whose monthly averages are between 10 °C and 26 °C. Annual precipitation ranges between 425 and 550 mm. Fieldwork was conducted in the northwestern part of the island in the area of La Vall.

The Balearic flora is composed principally of two large vegetal associations: *Quercetum ilicitum* and *Oleo Ceratonion* (Cardona 1979). On Minorca, the dominant forest type is Aleppo pine (*Pinus halepensis*) and holm oak (*Quercus ilex*). Woodlands make up 28 % of the island area with Aleppo pine predominating (83 % of woodland area) (Ministerio de Agricultura 1986). Mediterranean shrublands (*Olea europaea, Pistacia, Erica, Cistus, Phillyrea* spp.) form 9 % of Minorca and cultivated land constitutes more than half of the island.

The Cantabrian Mountains are situated on an east-west axis parallel and adjacent to the Bay of Biscay in northern Spain. They extend for 300 km and occupy an area of approximately 18,000 km^2. The physiography is rugged and elevations range from 600 m to 2500 m. The climate is continental; mean temperatures for the coldest and warmest months range from 0.5 °C (January) to 18 °C (August). Snow is present from January to March and mean precipitation averages 1400 mm. Pine marten faeces were collected in the Riaño, Fuentes Carrionas, Degaña and Somiedo National Hunting Reserves.

The Cantabrian flora is composed of Eurosiberian and Mediterranean vegetation communities. Fragmented stands of mixed deciduous forest occur primarily at middle and low elevations. The forest is composed primarily of durmast oak (*Quercus petraea*), pyrenean oak (*Q. pyrenaica*), and beech (*Fagus sylvatica*) with dispersed stands of birch (*Betula celtiberica*), rowan (*Sorbus aucuparia*), whitebeam (*S. aria*) and hawthorn (*Crataegus monogyna*). Regenerating shrublands (*Genista, Cytisus, Erica, Calluna* spp.) and open pasture cover 70 % of the vegetated area.

Methods

Faeces were collected periodically along foot trails in Minorca between February 1990 and March 1991, and in the Cantabrian Mountains from February to December 1990. Those that might have been confused with other small carnivores were discarded. Deposition dates were estimated to < 2 months and recorded for each respective time period. I sampled six bi-monthly periods in Minorca and three seasonal periods in the Cantabrian Mountains, Spring (15 February–31 May), Summer (1 June–15 September), and Autumn (16 September–30 November). For comparative purposes, Minorcan data also were presented by season as the food category totals for the following bi-monthly periods were averaged: Spring (March–April and May–June), Summer (May–June and July–August), Autumn (September–October and November–December), Winter (January–February).

Procedures for faeces analysis followed the standard techniques of washing, separating and identifying of different food items (Korschgen 1980; Reynolds and Aebischer 1991). Mammalian and avian prey remains were identified by microscopic and macroscopic analysis of hair, teeth, bones and feathers (Day 1966) and compared to a reference collection at the University of León. The identified food items were placed in one of seven food categories: mammals, birds, reptiles, amphibians, insects, plant material and other material (beeswax, human debris, etc.). An ocular estimate of percentage volume of each food item was made, and pooling data from all samples, the mean percentage volume and frequency of occurrence of each category of food item was calculated. Because analysis of remains by percent volume of faeces was found to be most correlated with the actual weight of prey eaten (Zielinski 1986), this method of analysis was used to describe the pine martens diet. Bi-monthly and seasonal differences in diet were assessed by X2 testing for homogeneity of variances for the major food categories (Sokal and Rohlf 1981).

I calculated the following trophic measures for the pine marten diet in Minorca and the Cantabrian Mountains as described in this study, in addition to data collected from the Spanish Pyrenees (Ruiz-Olmo and Lopez-Martin 1992) and a combined Cantabrian/Pyrenean data set (Cuesta et al. 1992).

The standardized feeding niche breadth was calculated for the respective number of food categories ("other material" not included) according to the niche breadth formula of Levins (1968), where pi is the proportion of food item i in the total diet:

$$\text{Feeding niche breadth} \quad B = (\Sigma Pi^2)^{-1}$$

The standardized niche breadth was calculated according to Hespenheide (1975), where n = the number of food categories identified. Bs increases as the diet becomes more generalized, and reaches 1.0 when all foods are exploited equally.

$$\text{Standardized niche breadth} \quad Bs = (B-1)/(n-1)$$

Niche breadths from Minorca were computed for the same 3-season period as the Cantabrian sample. To test whether niche breadth may be a function of sample size, faeces also were randomly selected from the island sample to equal that of the mainland data.

The indices for the mean prey size exploited by both pine marten populations were calculated according to the formula and approximate prey weights used by ERLINGE (1987), where fi denotes the frequency of occurrence of prey item i, and wi is the body weight of prey item i. All mammal prey of European pine marten (domestic goat and "unknown mammal" not included) were used with their respective weights, and all avian prey (total contribution) in the diet were assigned a standard weight of 40 g. In this calculation, no distinction was made among male-female and adult-juvenile mammal prey.

$$\text{Mean prey size index} = \Sigma fi \times wi$$

Average prey size was determined by multiplying the weight of each prey item by its number of appearances in the sample. A prey size index and mean prey size also were calculated for the Minorcan data for the three seasons using entire and equalized samples to determine whether they may be affected by sample size.

A distribution of prey body weights (g) was made by creating five categories (0–15; 16–50; 51–100; 101–300; >300) and computing the percent volume of each prey item among mammals and birds in the diet.

Results

Food habits

A wide array of food items were used by pine martens in both populations. In Minorca, a total of 22 identifiable food items were found in 1180 faeces analyzed, whereas the Cantabrian sample consisted of 28 food items from 193 faeces.

In Minorca, mammals and plant material were the most important foods (Fig. 1a). Mammals were consumed most during spring and winter (43 % and 39 % volume, respectively) while plant material was the predominant food type in autumn (64 %). During summer the pine marten diet was nearly equally divided among four of the five food categories with the avian component being greatest. The incidence of insects was highest among all food categories (44 % frequency of occurrence), but only constituted 19 % of the diet volume. Reptiles appeared in low quantities throughout the year.

Prey items varied in size from beetles (Coleoptera) to hedgehogs (*Erinaceus algirus*), rabbits (*Oryctolagus cuniculus*), and Herring gulls (*Larus argentatus*) (Tab. 1). Of special interest were the remains of an unidentified bat (Chiroptera) in one spring faeces and Mediterranean tortoise (*Testudo hermanni*) in 11 faeces throughout the year; the latter were juveniles in 10 of the 11 cases. The four principal components of the pine marten diet during the year were mammals, birds, insects, and plant material.

Mammals were taken all year round, however they were the dominant prey during

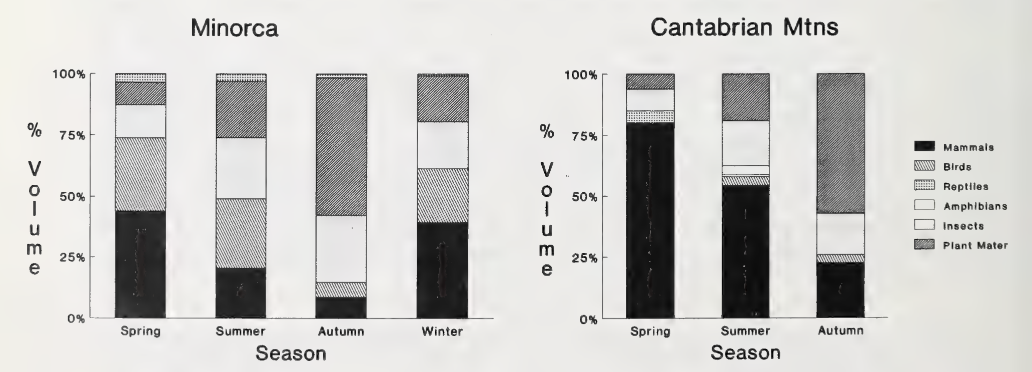


Fig. 1. Major food categories of pine marten diet arranged by seasonal averages in Minorca (N = 1180) and Cantabrian Mountains (N = 193)

Table 1. **Food items in faeces of Pine marten expressed as percent volume on the island of Minorca, Spain, March 1990–February 1991**
(Frequency of occurrence in parentheses)

	March–April (N = 293)	May–June (N = 174)	July–August (N = 307)	Sept–October (N = 98)	Nov–December (N = 116)	Jan–February (N = 192)	Total (N = 1180)
Mammals	58.4 (68.6)	27.4 (35.0)	13.5 (19.8)	8.2 (14.3)	11.9 (18.9)	46.7 (56.7)	31.8 (39.6)
Oryctolagus cuniculus	8.7 (10.9)	3.3 (3.4)	1.7 (2.2)	1.5 (2.0)	0.0 (0.0)	5.5 (6.2)	4.1 (5.0)
Rattus sp.	18.7 (20.8)	10.2 (12.0)	5.5 (7.8)	1.0 (1.0)	0.3 (4.3)	15.7 (17.7)	10.6 (12.3)
Eliomys quercinus	14.6 (16.7)	2.0 (2.8)	1.6 (1.9)	2.3 (3.0)	2.4 (2.6)	4.8 (5.7)	5.6 (6.5)
Apodemus sylvaticus	13.8 (16.4)	7.1 (9.7)	3.2 (4.5)	1.9 (4.1)	4.7 (8.6)	13.1 (18.2)	8.1 (10.8)
Mus sp.	2.2 (2.7)	0.8 (1.1)	0.6 (1.3)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.8 (1.1)
Crocidura suaveolens	0.0 (0.0)	0.5 (0.5)	0.1 (0.3)	0.9 (1.0)	0.0 (0.0)	0.0 (0.0)	0.2 (0.2)
Erinaceus algirus	0.0 (0.0)	0.0 (0.0)	0.3 (0.3)	0.0 (0.0)	0.0 (0.0)	0.5 (0.5)	0.1 (0.1)
Chiroptera	0.3 (0.3)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.1 (0.1)
Unknown mammal	0.1 (0.7)	3.3 (5.1)	0.4 (1.3)	0.4 (3.0)	1.8 (3.4)	6.9 (8.3)	1.9 (3.2)
Birds	18.2 (30.7)	39.6 (52.8)	17.3 (30.6)	5.0 (8.1)	8.9 (15.5)	23.6 (38.5)	20.1 (31.7)
Feathers	17.5 (27.6)	36.2 (47.7)	15.6 (25.5)	4.7 (7.1)	8.9 (15.5)	23.0 (37.0)	18.9 (28.5)
Egg fragments	0.7 (2.4)	3.0 (5.1)	1.7 (5.5)	0.3 (1.0)	0.0 (0.0)	0.5 (1.5)	1.2 (3.1)
Reptiles	0.9 (4.7)	6.0 (10.9)	0.3 (0.6)	2.5 (7.1)	1.3 (1.7)	0.1 (0.5)	1.5 (3.8)
Lacertidae	0.9 (4.7)	3.7 (8.0)	0.3 (0.6)	0.5 (1.0)	1.3 (1.7)	0.0 (0.0)	1.1 (2.7)
Testudo hermanni	0.0 (0.0)	2.3 (2.8)	0.0 (0.0)	2.0 (6.1)	0.0 (0.0)	0.1 (0.5)	0.5 (1.0)
Insects	9.2 (30.3)	17.5 (44.8)	32.2 (67.7)	23.0 (46.0)	8.7 (22.4)	19.2 (41.1)	19.2 (44.1)
Coleoptera	7.0 (25.6)	5.4 (21.8)	8.4 (8.8)	20.6 (38.7)	8.5 (20.7)	17.2 (34.3)	8.6 (22.7)
Orthoptera	0.3 (2.0)	9.3 (16.6)	28.6 (56.6)	2.3 (7.1)	0.1 (0.8)	1.9 (5.2)	9.5 (19.2)
Other invertebrates	1.8 (3.6)	2.5 (5.6)	0.9 (1.2)	0.0 (0.0)	0.1 (0.8)	0.1 (1.5)	1.1 (2.3)
Plant material	8.6 (15.0)	9.3 (16.6)	36.5 (65.7)	60.1 (80.6)	68.9 (81.9)	10.3 (14.5)	26.7 (40.4)
Ceratonia siliqua	2.8 (5.1)	7.7 (3.4)	2.8 (5.5)	33.8 (39.8)	49.3 (57.7)	7.3 (9.3)	10.7 (13.7)
Rubus ulmifolius	0.0 (0.0)	0.1 (0.5)	19.4 (35.5)	1.0 (1.0)	0.0 (0.0)	0.0 (0.0)	5.2 (22.6)
Ficus carica	0.0 (0.0)	2.7 (6.3)	7.9 (13.0)	2.4 (3.0)	0.0 (0.0)	0.0 (0.0)	2.7 (4.5)
Vitis vinifera	0.0 (0.0)	0.0 (0.0)	3.0 (6.2)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.8 (1.6)
Arbutus unedo	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	16.4 (19.8)	0.4 (0.5)	3.0 (4.2)
Rhamnus alaternus	0.0 (0.0)	0.5 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	1.7 (2.0)
Juniperus phoenicea	0.8 (1.0)	0.0 (0.0)	0.3 (0.3)	4.2 (5.1)	1.7 (1.7)	0.0 (0.0)	0.7 (0.9)
Myrtus communis	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	1.0 (0.0)	1.3 (1.7)	0.0 (0.0)	0.2 (0.2)
Gramineas	2.9 (5.8)	0.0 (0.0)	0.0 (0.0)	1.5 (2.0)	0.1 (0.8)	0.0 (0.0)	1.8 (1.7)
Other plant material	2.1 (3.0)	3.8 (5.6)	2.8 (5.8)	0.9 (2.0)	0.0 (0.0)	1.0 (3.6)	2.2 (3.8)
Other material	0.9 (1.3)	0.0 (0.0)	0.0 (0.0)	1.0 (1.0)	0.1 (0.8)	0.0 (0.0)	0.3 (0.5)

winter and early spring (January–February, March–April) comprising 52 % of the diet volume. All of the island mammal fauna appeared in the diet; the most frequently taken were rats (*Rattus* sp.) and wood mice (*Apodemus sylvaticus*). Plant material (primarily fleshy fruits) was the main food component during July–August (36 % of diet), September–October (60 %), and November–December (69 %); blackberries (*Rubus ulmifolius*) and figs (*Ficus carica*) were the preferred fruits during the first period and carob fruit (*Ceratonia siliqua*) in the second. The highest incidence occurred in early winter (November–December) where nearly half of the diet was composed of carob fruit; strawberry tree (*Arbutus unedo*) fruit also appeared frequently.

Birds were the most important food in early summer (May–June) comprising 39 % of the diet and also well represented in winter and early spring. Of 50 May–June faeces having feathers, 18 species were identified; 44 faeces (88 %) belonged to breeding species (N = 14; 72 %) while only 6 (12 %) were migratory (N = 4; 28 %) (Tab. 2). The remains of the breeding species were mostly nestlings. Eggshell fragments rarely appeared in the faeces analyzed, however during these two months they doubled in occurrence.

Table 2. **Breeding and migrant birds (X) found in Minorcan pine marten faeces during May–June, 1990**

Species	N	Breeding	Migrant
Larus argentatus	19	X	
Acanthis cannabina	1	X	
Carduelis carduelis	1	X	
Chloris chloris	2	X	
Columba livia	3	X	
Emberiza calandra	1	X	
Erithacus rubecula	1		X
Oenanthe oenanthe	1		X
Passer domesticus	1	X	
Phylloscopus trochilus	1		X
Phylloscopus sp.	3		X
Saxicola torquata	1	X	
Sylvia atricapilla	1	X	
Sylvia borin	1		X
Sylvia cantillans	1	X	
Sylvia melanocephala	8	X	
Sylvia sarda	3	X	
Turdus philomelos	1		X
Total	50	44 (88 %)	6 (12 %)

Insect consumption during the year was relatively uniform, peaking during summer (July–August) as grasshoppers (Orthoptera) composed 89 % of the total; otherwise beetles (Coleoptera) were the most consumed insects. Reptiles (Lacertidae and Mediterranean tortoise) were taken intermittently, primarily during early summer.

The bi-monthly diets in Minorca were extremely variable during the year. Highly significant differences ($P < 0.0001$, df = 4) were found between all periods except January–February and March–April, and September–October and November–December ($P > 0.01$, df = 4).

Three food categories dominated the Cantabrian pine marten diet during the three seasons, mammals, plant material and insects (Fig. 1b). Mammals were the most important component in the diet (56 %), followed by plant material (24 %) and insects (14 %). The remaining food categories (reptiles, birds and amphibians) were scarcely represented in the diet, and may be a result of the smaller sample size and period.

Prey items also were disparate in size and ranged from beetles and grasshoppers to red squirrels (*Sciurus vulgaris*) and hares (*Lepus* sp.) (Tab. 3). Trace remains of domestic goat appeared in the diet and most likely were taken as carrion. During spring and summer mammals were the dominant food component as they formed 79 % and 54 % of the diet volume, respectively. Of these, wood mice were taken most, followed by field mice (*Microtus agrestis*) and bank voles (*Clethrionomys glareolus*). In autumn, plant material was most important and occupied 57 % of the diet, primarily due to the nearly exclusive consumption (97 % of plant material) of rowan berries. Other fruits eaten by pine martens, although rarely, included: hawthorn, blackberries, alpine buckthorn (*Rhamnus alpinus*).

Table 3. **Food items in faeces of Pine marten expressed as percent volume in the Cantabrian Mountains, Spain, 1990–1991**

(Frequency of occurrence in parentheses)

	Spring (N = 86)	Summer (N = 52)	Autumn (N = 55)	Total (N = 193)
Mammals	79.5 (97.6)	54.2 (80.7)	22.5 (34.5)	56.4 (75.1)
Apodemus sylvaticus	33.3 (44.1)	23.5 (36.5)	9.9 (16.3)	24.0 (34.2)
Apodemus flavicollis	1.1 (1.1)	0.0 (0.0)	0.0 (0.0)	0.5 (0.5)
Microtus agrestis	24.4 (27.9)	12.1 (13.4)	5.4 (9.0)	15.7 (18.6)
Clethrionomys glareolus	6.8 (7.0)	6.0 (11.5)	5.9 (5.4)	5.8 (7.7)
Eliomys quercinus	4.3 (5.8)	7.6 (9.6)	1.3 (1.8)	4.3 (5.7)
Arvicola terrestris	2.3 (2.3)	0.0 (0.0)	0.0 (0.0)	1.0 (1.0)
Pitymys lusitanicus	3.0 (3.5)	0.0 (0.0)	0.0 (0.0)	1.3 (1.5)
Mus musculus	1.1 (1.1)	0.0 (0.0)	0.0 (0.0)	0.5 (0.5)
Sorex coronatus	0.9 (1.1)	0.0 (0.0)	0.0 (0.0)	0.9 (2.1)
Crocidura russula	0.7 (1.1)	0.0 (0.0)	0.0 (0.0)	0.3 (0.5)
Sciurus vulgaris	0.0 (0.0)	0.0 (0.0)	1.8 (1.8)	0.5 (0.5)
Lepus sp.	0.3 (1.1)	0.0 (0.0)	0.0 (0.0)	0.1 (0.5)
Domestic goat	0.9 (1.1)	3.1 (3.8)	0.0 (0.0)	1.2 (1.5)
Birds	0.3 (1.1)	3.5 (3.8)	3.2 (5.4)	2.0 (3.1)
Feathers	0.3 (1.1)	3.5 (3.8)	3.2 (5.4)	2.0 (3.1)
Reptiles	4.9 (11.6)	0.8 (1.9)	0.0 (0.0)	2.4 (5.7)
Podarcis muralis	1.8 (4.6)	0.0 (0.0)	0.0 (0.0)	0.8 (2.1)
Podarcis sp.	1.5 (1.1)	0.0 (0.0)	0.0 (0.0)	0.1 (0.5)
Lacerta schreiberi	2.2 (3.5)	0.0 (0.0)	0.0 (0.0)	0.9 (1.5)
Coronella girondica	0.4 (2.3)	0.0 (0.0)	0.0 (0.0)	0.2 (1.0)
Lacertidae	0.0 (0.0)	0.8 (1.9)	0.0 (0.0)	0.2 (0.5)
Amphibians	0.0 (0.0)	3.7 (3.8)	0.0 (0.0)	0.9 (1.0)
Rana temporaria	0.0 (0.0)	1.9 (1.9)	0.0 (0.0)	0.9 (1.0)
Rana sp.	0.0 (0.0)	1.7 (1.9)	0.0 (0.0)	0.4 (0.5)
Insects	8.8 (29.0)	18.6 (36.5)	17.0 (32.7)	13.8 (32.1)
Coleoptera	8.7 (27.9)	15.1 (28.8)	14.2 (27.2)	12.0 (28.0)
Orthoptera	0.0 (0.0)	2.7 (5.7)	0.0 (0.0)	0.7 (1.5)
Hymenoptera	0.0 (0.0)	0.8 (1.9)	0.3 (1.8)	0.3 (1.0)
Unknown insects	0.1 (1.1)	0.0 (0.0)	2.3 (3.6)	0.7 (1.5)
Plant material	6.1 (9.3)	19.1 (32.4)	57.3 (78.1)	24.2 (35.2)
Sorbus aucuparia	0.0 (0.0)	0.0 (0.0)	55.6 (72.7)	15.9 (20.7)
Crataegus monogyna	4.3 (4.6)	0.0 (0.0)	0.0 (0.0)	1.9 (2.1)
Rubus ulmifolius	0.0 (0.0)	3.5 (5.7)	0.0 (0.0)	0.9 (1.5)
Rhamnus alpinus	0.0 (0.0)	2.7 (5.7)	0.0 (0.0)	0.7 (1.5)
Prunus sp.	0.0 (0.0)	2.9 (3.8)	0.0 (0.0)	0.7 (1.0)
Rosa sp.	0.0 (0.0)	0.0 (0.0)	0.3 (1.8)	0.1 (0.5)
Unknown fruit	0.3 (1.1)	3.5 (3.8)	0.0 (0.0)	1.1 (1.5)
Gramineae	0.1 (1.1)	0.0 (0.0)	0.0 (0.0)	0.1 (0.5)
Other plant material	1.3 (2.3)	6.4 (13.4)	1.3 (3.6)	2.6 (5.6)

Insects were common food items and were most prevalent in summer forming 18 % of the diet. Beetles comprised 87 % of all insect remains. Reptiles and birds were rarely taken during the three seasons as each formed less than 5 % of the diet volume.

As in Minorca, seasonal pine marten diets varied greatly in the Cantabrian Mountains as significant differences were found between all three periods ($P < 0.0001$, $df = 5$).

Feeding niche breadth

Standardized feeding niche breadth indices were calculated for both pine marten populations. The annual diet of the Minorcan pine marten consisted of five food categories; it exhibited the most generalized feeding pattern resulting in a niche breadth index of 0.754. Cantabrian pine marten foods composed five categories and the 3-season diet was markedly less generalized as the niche breadth measured 0.380. Sampling duration and intensity in Minorca appeared to have no effect on the feeding niche breadth. When the island data were analyzed with the sample period and size equal to the Cantabrian data, Minorcan niche breadth indices remained high, 0.751 and 0.793, respectively.

The niche breadth index from combined Cantabrian/Pyrenean food habits data (0.469) was higher than data presented herein for the Cantabrian population but well below the island indices. Data from the Pyrenees resulted in the lowest index of all (0.186).

Prey size

The prey size index for Minorcan pine martens measured 66.4 (a total of eight prey items consumed) compared to 23.7 for Cantabrian martens even though the latter exploited a greater number ($N = 13$) of prey species. A larger prey size index resulted (80.5; eight prey items) when the island data were analyzed for the same duration as the Cantabrian; however, a lower index was obtained (49.9; six prey items) when sample sizes were identical.

All three prey size indices for Minorcan pine martens were larger than those from the Pyrenees (12.0) and the combined Cantabrian/Pyrenean (47.4) data set.

Prey species consumed by Minorcan pine martens during the 12-month period were significantly larger (98.7 ± 3.7 [SE] g, $N = 803$) than those found in the Cantabrian diet (31.4 ± 2.9 [SE] g, $N = 148$) ($P < 0.0001$, Mann-Whitney U test). The same was true when sampling periods and sizes were equalized (98.0 ± 4.1 [SE] g, $N = 618$ and 77.0 ± 7.4 [SE] g, $N = 126$, respectively; $P < 0.0001$). There was no significant difference between the mean prey size in the three variations of the Minorcan diet ($P > 0.10$).

The average prey size from the insular population also was significantly larger ($P < 0.0001$) when compared to Pyrenean (44.3 ± 6.6 [SE] g, $N = 91$) and Cantabrian/Pyrenean (40.7 ± 6.7 [SE] g, $N = 162$) food habits data. Prey sizes were not significantly different among the three mainland populations ($P > 0.05$).

Distributions of body weight across categories of prey size were different between pine martens from Minorca and the mainland (Fig. 2). Prey weight distributions among the three different Minorcan diet analyses were not significantly different ($P > 0.10$, $df = 3$, Kolmogorov-Smirnov test); the greatest proportion of prey items were from the 101–300 g category. Prey weight distributions from the Cantabrian, Pyrenean, and combined Cantabrian/Pyrenean diets were significantly different from those from Minorca ($P < 0.001$) as more than 75 % of the mainland prey species weighed between 16–50 g. There were no significant differences in weight distribution among the three mainland diets ($P > 0.10$).

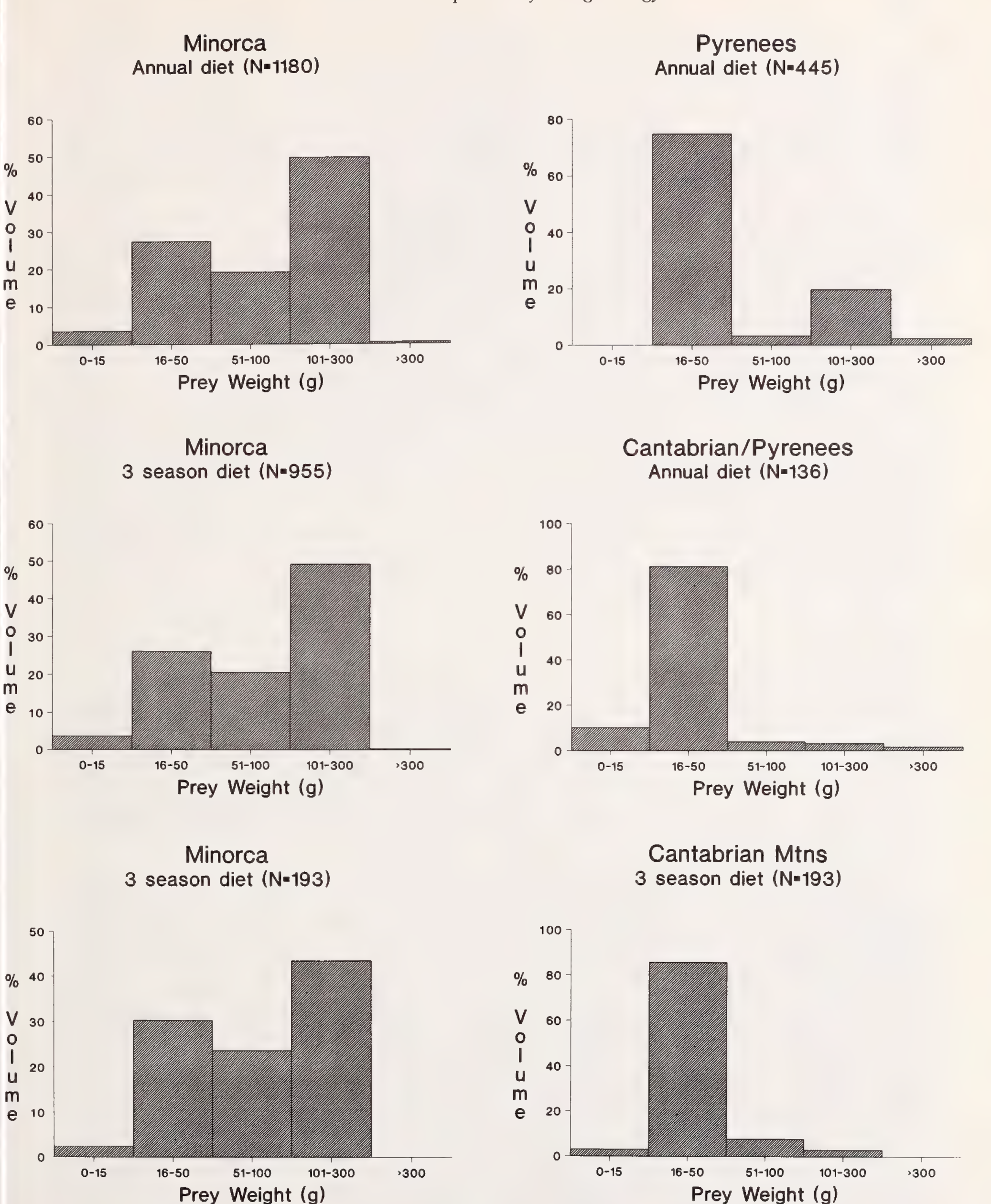


Fig. 2. Prey weight distributions from pine marten diets in Minorca and mainland Spain

Discussion

Feeding ecology

Interesting differences in diet can be seen between the two populations. The most striking result from the diet data is the nearly completely balanced use of food resources by pine martens in Minorca compared to the Cantabrian Mountains. Pine marten diet composition from the latter was comparable to diets reported in the Pyrenees (Ruiz-Olmo and López-Martín 1992) and Swiss Jura (Marchesi and Mermod 1989). The uniformity observed in the Minorcan pine marten diet may be explained by the insular environment and reduced competition whereby generalist feeders have been reported to capitalize on the increased availability of different kinds of foods and expanded resource base (see Lawlor 1982).

Reduced interspecific competition and increased food availability in insular communities generally selects for large individuals. Conversely, limited food supplies on small islands should select for small individuals (Wassersug et al. 1979; Lawlor 1982). Recently, a study of the geographic variation of adult pine martens (male and female combined) from Minorca, Majorca, and the Cantabrian Mountains revealed that Minorcan martens were significantly larger than the other two (6.2 % and 2.8 % larger, respectively), greater than any previously known population and proposed as a new subspecies, *M. m. minoricensis* (Alcover et al. 1986). Moreno et al. (1988) suggested that the Minorcan pine martens large size may be a result of higher predation on mammals and birds compared to Majorca, caused by the lack of competition with genets.

Several authors have pointed out the relationship between carnivore size and the size and abundance of their prey (Rosenzweig 1966; Case 1978; Simms 1979; Gittleman 1985; Vezina 1985). Erlinge (1987) reported that body size was positively correlated with prey size in European stoats (*M. erminea*). Shifts in body size in response to abundant prey have also been documented for other mustelids (McNab 1971; Powell and Brander 1977; King and Moody 1982; Monakhov 1989), canids (Schmitz and Kolenosky 1985; Geist 1987; Schmitz and Lavigne 1987; Thurber and Peterson 1991) and felids (Iriarte et al. 1990). Prey size indices and mean prey weights reported herein, however approximate, were significantly larger from Minorca than the Cantabrian Mountains, Pyrenees, and combined Cantabrian/Pyrenean data set.

Rabbits, rats and Herring gulls were important food items in Minorca unlike the other populations. Of some 37 faeces identified with Herring gull remains in Minorca, adult plumage appeared in 73 % (N = 27) while the rest were juveniles (Clevenger 1991). Similarly, King and Moody (1982) found a positive correlation between the size of introduced New Zealand stoats and the proportion of lagomorphs in the diet.

Lomolino (1985) reasoned that competitive release is a major factor responsible for insular gigantism in mammals, thereby suggesting that body size may be constrained by the presence of larger competitors (McNab 1971; Lawlor 1982). In communities where similar sized or larger competing species are absent, mean body size would be expected to increase (Rosenzweig 1968). On islands such as Minorca where the number of competitors is reduced, the range of food resources used by pine martens (its niche breadth) is amplified, greater prey sizes become available, which thereby may facilitate a shift to a larger mean body size (see Schoener 1967; Roughgarden 1972; Hespenheide 1975; Lister 1976). Prey species diversity is lower in insular vs. mainland environments, nonetheless overall prey abundance and availability may be greater in the former. Size differences between New Zealand and British stoats were explained by differences in overall prey size distribution for the two populations, although more species occur in Britain (King and Moody 1982).

Body size variation among continental and insular weasel populations showed no support for character displacement (Ralls and Harvey 1985; Erlinge 1987); however, in the Pacific Northwest large body sizes of American pine marten (*M. americana*) were

reported on islands with reduced interspecific competition (GIANNICO and NAGORSEN 1989). In the same population (NAGORSEN et al. 1991), a subsequent study did not reveal anything in the winter diet which could account for the distinct cranial morphology, but the authors noted that their one-season data were speculative. The large body size and absence of competitors in Minorca compared to mainland populations is concordant with this insular body size trend and supported by the diet and feeding ecology data presented herein.

FOSTER (1963) reported that island stone marten (*M. foina*) in the Mediterranean were smaller than individuals from the mainland. Dwarfism also has been documented among genets and the presently extinct stone marten from the Balearic Island of Ibiza (DELIBES 1977; DELIBES and AMORES 1986). If resource limitation is a major factor affecting insular body size of mammals, then differing levels of resource abundance (or competition) on Mediterranean islands may explain these trends. Information on variations in prey abundance among island and continental populations, and how conspecifics partition these resources is lacking. Answers to these questions will be necessary before critical tests can be carried out investigating island-mainland body size trends.

Like other marten studies have shown, food choice is determined by what is abundant and accessible (WECKWERTH and HAWLEY 1962; BRAINERD 1990). Minorcan pine marten concentrated on seasonally abundant foods or those that had the greatest energy return, evidenced by the high proportion of birds during May–June, and insects and fruit during July–December. The generalist feeding pattern was congruent with other European studies (LOCKIE 1961; NYHOLM 1970; PULLIAINEN 1981; WARNER and O'SULLIVAN 1982; MARCHESI and MERMOD 1989).

The highest consumption of mammals occurred between January–April, while predation was lower the remainder of the year. Seasonal data on small mammal abundance and availability from Minorca are forthcoming and I suspect like other studies have shown, that rodent population levels do not peak until late summer or autumn (GOSZCZYNSKI 1977; ERLINGE et al. 1983, 1984; ALIBHAI and GIPPS 1985; FLOWERDEW 1985). If so, then pine marten may exploit small mammals these months because other foods (birds, insects, fruit) are more scarce. Birds were taken all year-round, however, they were most prevalent in the diet during May–June, which earlier was shown to coincide with the hatching and fledgling period for most passerines in Minorca.

Mammals were the most important Cantabrian pine marten food during the 3-season period and were most prevalent in spring and summer. Other studies have also shown the importance of mammals in the species diet (LOCKIE 1961; NYHOLM 1970; DE JOUNGE 1981; PULLIAINEN 1981; REIG and JEDRZEJEWSKI 1988; JEDRZEJEWSKI et al. 1989; MARCHESI and MERMOD 1989). Wood mice were taken most, contrary to the aforementioned studies where microtine rodents predominated. The high incidence of woodland rodents suggests that Cantabrian pine marten forage primarily in beech/oak forests and less frequently in open habitats. In the Spanish Pyrenees woodland rodents were also preferred during spring and summer (RUIZ-OLMO and LÓPEZ-MARTÍN 1992). In autumn fruits replaced mammals in the Cantabrian diet which was found in other pine marten studies ((LOCKIE 1961; MARCHESI and MERMOD 1989).

In this paper I have reported on pine marten feeding ecology from one insular and one mainland population, in addition to food niche breadths and prey size selection from other mainland populations in Spain. More basic diet data is needed from island and mainland populations to conduct critical testing to determine if gigantism is a general phenomenon among insular pine martens and carnivores in general.

Acknowledgements

Appreciation is extended to C. Campos, M. A. Campos, A. Onrubia and R. Triay for assistance in the field and laboratory. F. J. Purroy identified the avian prey remains, J. Mayol and R. Squella provided logistical support, and J. and A. Teinturier kindly allowed me to use their house while in Minorca. I thank W. J. Zielinski for his comments and discussion on an earlier version of the manuscript. This work was partially supported by a grant from Spain's Ministry of Education and Science and the Gobierno Balear (Servei de Conservació de la Naturalesa).

Zusammenfassung

Vergleichende Nahrungsökologie des Baummarders (Martes martes Linné, 1758) bei einer Insel- und einer Kontinentalpopulation in Spanien

An Kotproben wurde die Zusammensetzung der Nahrung des Baummarders (*Martes martes*) bei einer Insel- (Menorca, Balearen) und einer Kontinentalpopulation (Kantabrisches Gebirge) über einen Zeitraum von einem Jahr bestimmt und miteinander verglichen. Dazu dienten folgende Parameter: Nahrungsspektrum, Breite der Nahrungsnische, Beutegrößenindex und Verteilung der Beutegewichte. Kleinsäuger, Vögel, Früchte und Insekten stellten die wichtigsten vier Nahrungskomponenten in beiden Populationen dar. Auf Menorca waren alle vier über das Jahr verteilt in ausgewogener Weise bedeutend, während im Kantabrischen Gebirge Kleinsäuger und Früchte jahreszeitlich dominierten. Darüber hinaus waren die Inselmarder durch eine deutlich größere Breite der Nahrungsnische gekennzeichnet. Sie nutzten alle Nahrung im Jahr annähernd gleichartig im Gegensatz zu den Mardern des Kantabrischen Gebirges und gegenüber Vertretern aus zwei weiteren kontinentalen Populationen. Beutegrößenindex und mittlere Beutegröße waren auf der Insel ebenfalls größer. Für Baummarder von Menorca ist im Vergleich mit Individuen vom Kontinent eine deutliche Zunahme der Körpergröße festgestellt worden. Dieser „Inselgigantismus" wird in Zusammenhang mit erweiterter Nahrungsabundanz auf Menorca und reduzierter interspezifischer Konkurrenz diskutiert.

References

Ministerio de Agricultura (1986): Mapa de cultivos y aprovechamientos de la provincia de Baleares. Madrid: Min. Agri., Pesca y Aliment.

Alcover, J. A.; Delibes, M.; Gosálbez, M.; Nadal, J. (1986): *Martes martes* Linnaeus, 1758, a les Balears. Misc. Zool. **10**, 323–333.

Alibhai, S. K.; Gipps, J. H. W. (1985): The population dynamics of bank voles. The ecology of woodland rodents: bank voles and wood mice. Zool. Soc. Lond. Symp. **55**, 277–305.

Brainerd, S. M. (1990): The pine marten and forest fragmentation: a review and general hypothesis. Trans. Intern. Game Biol. Congr. **19**, 421–434.

Cardona, M. A. (1979): Enciclopèdia de Menorca, II. El mon vegetal. Mahón: Obra Cultural de Menorca.

Case, T. J. (1978): A general explanation for insular body size trends in terrestrial vertebrates. Ecology **59**, 1–18.

Clevenger, A. P. (1991): Ecología de la marta (*Martes martes* L.) en los espacios naturales de las Islas Baleares. Doc. Tec. de Conserv. No. 7. Palma de Mallorca: Gov. Balear, Consell. d'Agri. i Pesca.

— (1992): Spring and summer food habits and habitat use of the European pine marten (*Martes martes* L.) on the island of Minorca, Spain. J. Zool. (London) (in press).

Cuesta, L.; Aymerich, M.; Palacios, F.; Garzon, J. (1992): Estudio comparativo de la alimentación de la marta y la garduña en su área de simpatría en la Península Ibérica. Doñ. Acta Vert. (in press).

Day, M. G. (1966): Identification of hair and feather remains in the gut and faeces of stoats and weasels. J. Zool. (London) **148**, 201–217.

Delibes, M. (1977): Sobre las ginetas de la Isla de Ibiza (*Genetta genetta isabelae* n. ssp.). Doñ. Acta Vert. **4**, 139–160.

Delibes, M.; Amores, F. (1986): The stone marten, *Martes foina* (Erxleben 1777) (Mammalia, Carnivora) from Ibiza (Pityusic, Balearic Islands). Misc. Zool. **10**, 335–345.

Erlinge, S. (1986): Specialists and generalists among the mustelids. Lutra **29**, 5–11.

— (1987): Why do European stoats *Mustela erminea* not follow Bergmann's rule? Holarct. Ecol. **10**, 33–39.

Erlinge, S.; Göransson, G.; Hansson, L.; Högstedt, G.; Liberg, O.; Nilsson, I. N.; Nilsson, T.; von Schantz, T.; Sylvén, M. (1983): Predation as a regulating factor on small rodent populations in southern Sweden. Oikos **40**, 36–52.

Erlinge, S.; Göransson, G.; Högstedt, G.; Jansson, G.; Liberg, O.; Loman, J.; Nilsson, I. N.;

von Schantz, T.; Sylvén, M. (1984): Can vertebrate predators regulate their prey? Am. Nat. **123**, 125–133.

Flowerdew, J. R. (1985): The population dynamics of wood mice and yellow-necked mice. The ecology of woodland rodents: bank voles and wood mice. Zool. Soc. Lond. Symp. **55**, 315–332.

Foster, J. B. (1963): The evolution of the native land mammals of the Queen Charlotte Islands and the problem of insularity. Ph. D. thesis, Univ. British Columbia, Vancouver.

Geist, V. (1987): Bergmann's Rule is invalid. Can. J. Zool. **65**, 1035–1038.

Giannico, G. R.; Nagorsen, D. W. (1989): Geographic and sexual variation in the skull of Pacific coast marten (*Martes americana*). Can. J. Zool. **67**, 1386–1393.

Gittleman, J. L. (1985): Carnivore body size: Ecological and taxonomic correlates. Oecologia **67**, 540–554.

Goszczynski, J. (1977): Connections between predatory birds and mammals and their prey. Acta Theriol. **22**, 399–430.

Hespenheide, H. A. (1975): Prey characteristics and predator niche width. In: Ecology and Evolution of Communities. Ed. by M. L. Cody and J. M. Diamond. Cambridge, Massachusetts: Harvard University Press. Pp. 158–180.

Iriarte, J. A.; Franklin, W. L.; Johnson, W. E.; Redford, K. H. (1990): Biogeographic variation of food habits and body size of the America puma. Oecologia **75**, 185–190.

Jedrzejewski, W.; Jedrzejweski, B.; Szymura, A. (1989): Food niche overlaps in a winter community of predators in the Bialowieza primeval forest, Poland. Acta Theriol. **34**, 487–496.

Jounge, J. de (1981): Predation of the pine marten, *Martes martes* L., in relation to habitat selection and food abundance during winter in central Sweden. Swed. Environ. Prot. Bd. Rept. 1401.

King, C. M.; Moody, J. E. (1982): The biology of the stoat (*Mustela erminea*) in the National Parks of New Zealand III. Morphometric variation in relation to growth, geographical distribution, and colonisation. New Zeal. J. Zool. **9**, 81–102.

Korschgen, L. J. (1980): Procedures for food habits analyses. In: Wildlife Management Techniques Manual. Ed. by D. Schemnitz. Washington, D. C.: The Wildlife Society. Pp. 113–127.

Lack, D. (1942): Ecological features of the bird faunas of British small islands. J. Anim. Ecol. **11**, 9–36.

Lawlor, T. E. (1982): The evolution of body size in mammals: evidence from insular populations in Mexico. Am. Nat. **119**, 54–72.

Levins, R. (1968): Evolution and changing environments. Princeton, New Jersey: Princeton University Press.

Lister, B. C. (1976): The nature of niche expansion in West Indian Anolis lizards. I: Ecological consequences of reduced competition. Evol. **30**, 659–676.

Lockie, J. D. (1961): The food of the pine marten (*Martes martes*) in west Ross-shire Scotland. Proc. Zool. Soc. Lond. **136**, 187–195.

Lomolino, M. V. (1985): Body size of mammals on islands: the island rule reexamined. Am. Nat. **125**, 310–316.

Marchesi, P.; Mermod, C. (1989): Regime alimentaire de la martre (*Martes martes* L.) dans le Jura suisse (Mammalia: Mustelidae). Rev. Suisse Zool. **96**, 127–146.

McNab, B. K. (1971): On the ecological significance of Bergmann's Rule. Ecology **52**, 845–854.

Monakhov, V. (1989): Morphological changes in sable *Martes zibellina* in consequence of introduction. In: Populationsökologie marderartiger Säugetiere. Ed. by M. Stubbe. Halle: Wiss. Beitr. Univ. Halle. Pp. 466–472.

Moreno, S.; Rodríguez, A.; Delibes, M. (1988): Summer foods of the pine marten (*Martes martes*) in Majorca and Minorca, Balearic Islands. Mammalia **52**, 289–291.

Nagorsen, D. W.; Campbell, R. W.; Giannico, G. R. (1991): Winter food habits of marten, *Martes americana*, on the Queen Charlotte Islands. Can. Field-Nat. **105**, 55–59.

Nyholm, E. (1970): On the ecology of the pine marten (*Martes martes*) in Eastern und Northern Finland. Suomen Riista **22**, 105–118.

Powell, R. A.; Brander, R. B. (1977): Adaptations of fishers and porcupines to the predator prey system. Proc. 1975 Pred. Symp. Univ. Montana, Missoula.

Pulliainen, E. (1981): Food and feeding habits of the pine marten in Finnish Forest Lapland in winter. In: Worldwide Furbearer Conference Proceedings. Ed. by J. Chapman and D. Pursley. Frostburg, Maryland. pp. 580–598.

Ralls, K.; Harvey, P. H. (1985): Geographic variation in size and sexual dimorphism of North American weasels. Biol. J. Linn. Soc. **25**, 119–167.

Reed, T. R. (1982): Interspecific territoriality in the chaffinch and great tit on islands and the mainland of Scotland: playbacks and removal experiments. Anim. Behav. **30**, 171–181.

Reig, S.; Jedrzejweski, W. (1988): Winter and early spring food of some carnivores in the Bialowieza National Park, eastern Poland. Acta Theriol. **33**, 57–65.

Reynolds, J. C.; Aebischer, N. J. (1991): Comparison and quantification of carnivore diet by faecal analysis: a critique with recommendations, based on a study of the Fox *Vulpes*, Mamm. Rev. **21**, 97–122.

Rosenzweig, M. L. (1966): Community structure in sympatric carnivores. J. Mammalogy **47**, 602–620.
— (1968): The strategy of body size in mammalian carnivores. Amer. Midl. Nat. **80**, 299–315.
Roughgarden, J. (1972): Evolution of niche width. Am. Nat. **106**, 683–718.
Ruiz-Olmo, J.; López-Martín, J. M. (1992): Seasonal food of pine marten (*Martes martes* L., 1758) in a fir forest of Pyrenean Mountains (northeastern Spain). Proc. I European Congr. Mammal. Lisbon, Portugal.
Schmitz, O. J.; Kolenosky, G. B. (1985): Wolves and coyotes in Ontario: morphological relationships and origins. Can. J. Zool. **63**, 1130–1137.
Schmitz, O. J.; Lavigne, D. M. (1987): Factors affecting body size in sympatric Ontario *Canis*. J. Mammalogy **68**, 92–99.
Schoener, T. (1967): The ecological significance of sexual dimorphism in size in the lizard *Anolis conspersus*. Science **155**, 474–477.
Simms, D. A. (1979): North American weasels: resource utilization and distribution. Can. J. Zool. **57**, 504–520.
Sokal, R. R.; Rohlf, F. J. (1981): Biometry. San Francisco: W. H. Freeman.
Sondaar, P. Y. (1977): Insularity and its effect on mammal evolution. In: Major Patterns in Vertebrate Evolution. Ed. by M. K. Hecht, P. C. Goody, and B. M. Hecht. New York: Plenum Press. Pp. 671–707.
Thompson, I. D.; Colgan, P. W. (1987): Numerical responses of martens to a food shortage in northcentral Ontario. J. Wildl. Manage. **51**, 824–835.
Thurber, J. M.; Peterson, R. O. (1991): Changes in body size associated with range expansion in the coyote (*Canis latrans*). J. Mammalogy **72**, 750–755.
Vezina, A. F. (1985): Empirical relationships between predator and prey size among terrestrial vertebrate predators. Oecologia **67**, 555–565.
Warner, P.; O'Sullivan, P. (1982): The food of the pine marten *Martes martes* in County Clare. Trans. Intern. Game Biol. Congr. **14**, 323–330.
Wassersug, R. J.; Yang, H.; Sepkoski, Jr., J. J.; Raup, D. M. (1979): The evolution of body size on islands: a computer simulation. Am. Nat. **114**, 287–295.
Weckwerth, R. P.; Hawley, V. P. (1962): Marten food habits and fluctuations in Montana. J. Wildl. Manage. **26**, 55–74.
Wilson, D. S. (1975): The adequacy of body size as a niche difference. Am. Nat. **109**, 769–784.
Zielinski, W. J. (1986): Relating marten scat contents to prey consumed. Cal. Fish and Game **72**, 110–116.

Author's address: Anthony P. Clevenger, Departamento de Biología Animal, Universidad de León, E-24071 León, Spain

Z. Säugetierkunde 58 (1993) 225–231
© 1993 Verlag Paul Parey, Hamburg und Berlin
ISSN 0044-3468

Faecal marking behaviour by free-ranging Common genets *Genetta genetta* and Egyptian mongooses *Herpestes ichneumon* in southwestern Spain

By F. Palomares

Estación Biológica Doñana, Consejo Superior de Investigaciones Científicas, Sevilla, Spain

Receipt of Ms. 3. 6. 1992
Acceptance of Ms. 27. 12. 1992

Abstract

Studied defecation behaviour of the common genet and the Egyptian mongoose at the Doñana National Park from November 1985 to November 1989. Both species frequently used latrines and more than one individual contributed to latrine formation. Genets placed their latrines in trees situated on the edges of the more frequently used habitats, whereas mongooses defecated on the ground, and their latrines were found within preferred habitats, near to resting sites. Genets increased their marking behaviour in February–March and November–December, and mongooses in January–February and September–October. Latrine switching within the same area was observed in mongooses. Data tend to indicate that latrines are used as a communication tool in both species.

Introduction

Faeces seem to be used by many carnivores as a communication tool in their social lives (Macdonald 1980; Gorman and Trowbridge 1989). Nevertheless, little is known about faecal or scent marking behaviour in viverrids (Gorman and Trowbridge 1989), the only studies being on free-ranging civets, *Civettictis civetta*, (Beader and Randall 1978) and captive African dwarf mongooses, *Helogale undulata*, (Rasa 1973), meerkats, *Suricata suricata*, (Moran and Sorensen 1986), water mongooses, *Atilax paludinosus*, (Baker 1988) and common genets, *Genetta genetta*, (Roeder 1980a). Furthermore, faecal marking behaviour is discussed only occasionally in some of these studies. Here, some aspects of faecal marking behaviour by free-ranging common genets and Egyptian mongooses, *Herpestes ichneumon*, in the Doñana National Park (southwestern Spain) are described.

Study area

The study was carried out in two areas of the Doñana National Park: the Biological Reserve and the Coto del Rey. The Park is situated on the western bank of the Guadalquivir River mouth, in southwestern Spain (approximately 37 °N, 6°30′W), and includes three main biotopes: marshes or marismas, scrubland and dunes. The marshes are usually flooded in winter and covered by *Scirpus* sp. There are two main types of scrubland: a dry, xerophytic scrubland vegetated by *Halimium* sp. and *Rosmarinus* sp., and a dense, mesic scrubland with *Erica* sp. and *Calluna vulgaris*. There are scattered cork oaks (*Quercus suber*) all over the scrubland. In the dunes, there are mobile bare sand dunes with valleys between, which typically are colonized by pine (*Pinus pinea*) forests. The climate is Mediterranean subhumid, characterized by dry, hot summers and mild, wet winters.

The Biological Reserve (6700 ha) is situated in the middle of the Park, and the three main biotopes described above for the Park can be found. The Coto del Rey, of 3500 ha, is situated in the northern part of the Park, and is characterized by pines and *Eucalyptus* sp. forestations on the matorral, and abundant *Pistacia lentiscus* patches where the ground water table is nearer the surface.

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5804-0225 $ 02.50/0

Material and methods

The Biological Reserve was examined fully for genet defecation sites, special attention being paied to trees and *Erica* and *Calluna* scrubland (the main habitat of the species in the study area; Palomares and Delibes 1988). By contrast, three areas of the Biological Reserve (Caño de la Raya = CR, Lucio Bolín = LB, and Laguna Santa Olalla = LO), where mongooses were radio-tracked (Palomares and Delibes 1991a), were examined for mongoose faeces. Greater searching effort was undertaken from November 1985 to January 1986. Each defecation site was marked on the terrain. A site was considered as a latrine if there were 2 or more faeces. Latrines were periodically sampled (weekly from November 1985 to April 1986, and monthly from then to January 1987). In total, 264 and 141 samplings were carried out on genet and mongoose latrines, respectively. Radio-tracking at the Biological Reserve of 2 genets (an adult dispersing male, and a young female) and 4 mongooses (2 adult and 2 young females) from September 1985 to April 1986 (Palomares and Delibes 1988, 1991a) helped to interpret some of the results on faecal marking behaviour. Habitat type where latrines were found and their situation with respect to places commonly used by radio-tracked individuals were noted.

All faeces were collected for diet analysis (Palomares and Delibes 1991b), but their number and position were noted before collecting. To test possible influences of faecal removal on genet marking behaviour, some faeces were left at the latrine on 64 sampling occasions, whereas in another 200 occasions all of the faeces were collected. Removal did not affect presence or absence of faeces on the following sampling occasion (G-test of independence; $G = 0.002$, $p < 0.001$).

Genet latrines were also intensively searched for during June 1987 in the Coto del Rey. Sporadic information on marking behaviour of both species was also obtained from March 1987 to November 1989 while radio-tracking 24 mongooses and 10 genets and collecting faeces for scat analysis in the same area (Palomares and Delibes 1991a).

Results

Both genets and mongooses made latrines. Twenty-seven genet defecation sites were found on the Biological Reserve, with a number of faeces ranging from 1 to 27. Seven of these sites contained only 1 scat; fifteen were periodically sampled. More than one genet seemed to use the latrines. The radio-tracked male was trapped at latrine 320, which was continuously used (Tab. 1) despite the fact that this individual never returned to the area during 5 months of radio-tracking (Tab. 1).

Forty-one mongoose defecation sites were found on the Biological Reserve, with a number of faeces ranging from 1 to 40. Twenty-one of these sites had only 1 scat; fifteen were periodically sampled. Different mongooses also deposited their faeces on the same latrine. On 6 January 1985, 2 mongooses (an adult radio-tracked female and an untagged animal) left 3 faeces a few centimeters from each other, close to a resting site. At the Coto del Rey I observed numerous latrines used by different mongooses belonging to the same family group.

Defecation site ground

Genet faeces were found in trees (44.4 % on main trunks, 22.2 % on secondary trunks, 14.8 % on raptor nests and 7.4 % on tree branches), on thickets or hedges (7.4 %) and on the ground (3.7 %; n = 27 sites). Faeces in trees were situated on average 4.2 m high (SD = 2.8, range = 2.5–14.0, n = 22). Trees were always cork oaks except for one pine.

When using latrines, genets tended to deposit faeces over the whole available surface and, as a rule, fresh faeces were never deposited over other fresh ones, although over old ones. The only latrine found on the ground had 9 faeces deposited over semifallen rush bushes with the furthest separated by 25 m.

At least 100 cork oaks were searched for genet latrines in the Coto del Rey, but none were found. On the other hand, only 3 latrines (with 3, 6 and 21 faeces) used for a few days were found in this area during radio-tracking activities. Scattered faeces were sometimes found, all of them situated on the ground.

Table 1. **Number of faeces by month and latrine in common genets from November 1985 to January 1987**

Latrine number	Months														
	NO	DE	JA	FE	MA	AP	MA	JU	JU	AG	SE	OC	NO	DE	JA
320	20[a]	7[a]	4	5	4	3	2	2	1	3	23	18	8	2	2
215	3[a]	0[a]	0	0	0	0	0	0	0	0	0	0	1	0	0
204	0[a]	2[a]	1	0	1	0	0	0	0	0	1	0	1	2	3
308		19[a]	4	0	0	0	0	0	0	0	0	0	4	7	1
306		8[a]	2	3	2	1	1	4	0	0	0	0	0	0	0
314		5[a]	0	2	0	0	0	0	0	0	0	0	1	0	0
210		3[a]	1	0	1	0	0	0	0	0	0	0	1	0	1
415		3[a]	0	2	0	0	0	0	0	0	0	0	0	–	–
281			9[a]	1	8	0	0	0	0	0	0	0	0	0	0
200			6[a]	0	0	0	0	0	0	0	0	0	0	0	0
300			27[a]	4	12	4	3	1	6	0	0	1	3	7	4
261			8[a]	3	1	0	0	0	0	0	0	0	0	0	0
418			14[a]	8	4	0	0	3	13	1	0	1	2	3	2
388						3[a]	0	0	0	2	0	2	8	7	4
282									4[a]	1	0	0	0	0	0
Mean			1.5	2.2	2.5	0.6	0.4	0.7	1.4	0.5	1.6	1.5	1.9	2.0	1.2
SD			1.7	2.4	3.7	1.3	0.9	1.3	3.7	0.9	5.9	4.6	2.7	2.9	1.5

[a] these data were not used to obtain the monthly mean.

All mongoose faeces were found on the ground. Of 17 latrines, 35.3 % were by bramble edges or other thick vegetation; 23.5 % under this same thick vegetation; 17.6 % under pine shrubs, but clearly visible; 11.8 % over flattened grass and surrounded by rushes, *Juncus* sp.; 5.9 % on paths among vegetation; and 5.9 % at an open ground elevation in the middle of a pool. Most of the detected latrines (76.5 %) were in clearly visible sites, whereas 23.5 % were hidden. However, dense vegetation probably made it difficult for the observer to find the latter. Scattered faeces were mainly found on the middle of paths within the most used habitats and on those leading to resting sites.

In mongooses, latrine surface sizes varied greatly, from those with faeces separated by a few centimeters, to others where there was a continuum of faeces with the furthest separated by 45 m.

Place of latrines

Genets mainly inhabit mesic scrubland patches in the Biological Reserve (Palomares and Delibes 1988) and preferentially deposited their faeces on the edges of these patches (69.2 %; n = 26; $X^2 = 3.85$, $p = 0.0498$). Inside the 1.4 km^2 of the female home range (the only individual that had a defined range; Palomares and Delibes 1988), three latrines were found, situated by the edges of mesic scrubland.

Mongooses use mesic scrubland and brambles (*Rubus* sp.) to rest (Palomares and Delibes 1990) and most faeces were found very near or inside this habitat. Thirteen of 17 latrines (those with higher number of faeces and used longer) were less than 50 m from known nocturnal resting sites and inside home range core areas of radio-tracked individuals. During intensive 24-hour tracking periods mongooses were observed on 5 occasions defecating close to resting sites. The number of latrines in the home ranges of the three most radio-tracked mongooses were 6 (home range of 1.7 km^2), 7 (home range of 4.8 km^2) and 2 (home range of 5.7 km^2).

Temporal pattern of latrine use

On average, the number of faeces at genet latrines was higher in February–March and November–December, and lower from April to August, with a slight increase in July (Tab. 1). Of 15 latrines periodically sampled, only 5 were continuously used for at least 4 months, and only 1 was always used (Tab. 1). Two latrines (one with 9 faeces on the ground and another with 15 faeces in a raptor nest) made by the radio-tagged male while roaming by the dunes were located. They were close to resting sites. When resting sites were deserted, the latrines were not used any longer.

Numbers of faeces on mongoose latrines were higher in September–October and February, with lower but similar numbers for the rest of the year (Tab. 2). Usually mongooses did not keep latrines for long. Latrines were commonly used during an isolated month, or at most, for 2 or 3 consecutive months, although after a time they could be re-used. Two latrines were used during 7 months (Tab. 2).

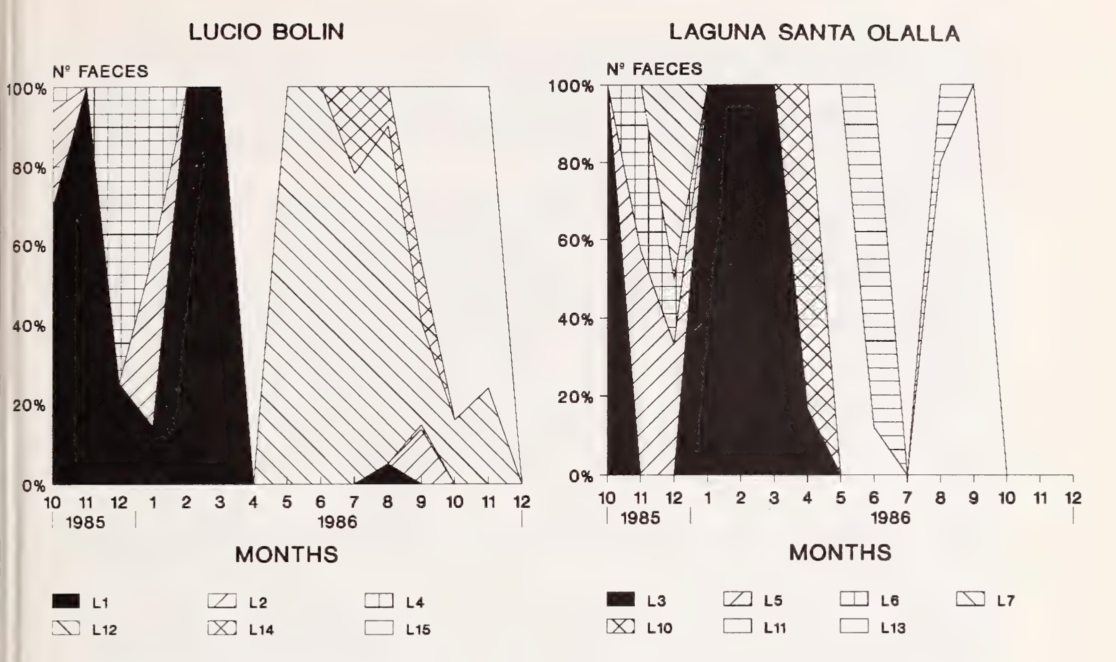
Table 2. **Number of faeces by month and latrine in Egyptain mongooses from November 1985 to January 1987**

Latrine		Months														
N°	Place	OC	NO	DE	JA	FE	MA	AP	MA	JU	JU	AG	SE	OC	NO	DE
1	B	23	2	2	1	1	1	0	0	0	0	1	0	0	0	0
2	B	8	0	0	3	0	0	0	0	0	0	0	12	0	0	0
3	O	3	0	0	1	1	1	1	0	0	0	0	0	0	0	0
4	B	2	0	6	3	0	0	0	0	0	0	0	1	0	0	0
5	O		4	2	0	–	–	–	–	0	0	0	–	–	–	–
6	O		3	1	0	–	–	–	–	0	0	0	–	–	–	–
7	O			3	0	–	–	–	–	0	0	0	–	–	–	–
8	CR				20	0	0	0	0	0	0	0	0	0	0	0
9	CR					26	13	9	0	0	0	0	0	1	0	0
10	O							5	0	0	0	0	0	0	0	0
11	O								11	3	0	4	1	0	0	0
12	B								9	6	32	17	23	6	5	0
13	O									22	0	1	–	–	–	–
14	B										9	2	13	0	0	0
15	B												40	32	16	[a]
Mean		9.0	1.5	2.0	3.5	4.7	2.5	2.1	2.2	2.4	2.9	1.8	8.2	3.5	1.9	0.0
SD		9.7	1.8	2.1	6.8	10.5	5.2	3.5	4.4	6.2	8.7	4.5	13.5	9.6	4.9	0.0

B = Lucio Bolin, O = Laguna Santa Olalla, CR = Caño de la Raya.
[a] Latrine was flooded.

Latrine switching by mongooses

Mongooses seemed to use latrines alternatively on a same area. For instance, at Bolin, latrine 1 was the most used from October 1985 to March 1986, together latrines 2 and 4; latrine 12 was the most used from May to August 1986, and although mongooses never stopped defecating on latrine 12, latrine 15 was the most used from September to November 1986 (see Fig.). At Olalla, latrines 3, 5, 6 and 7 were the most used from the beginning of the study to April 1986, but from May on, only latrines 11 and 13 were used (Fig.).



Monthly contribution of each latrine (L) to total number of faeces collected of Egyptian mongooses in Lucio Bolin and Laguna Santa Olalla, both in the Doñana Biological Reserve

Discussion

The use of faeces for communication has been widely suggested in several carnivore species (MACDONALD 1980; GORMAN and TROWBRIDGE 1989), and this might be also the case for genets and mongooses since they used latrines situated at specific places. ROEDER (1980a) concluded that captive genets use their faeces for exchanging information, and HEFETZ et al. (1984) found a specific component in the substance secreted by the perianal gland of male Egyptian mongooses. The position of this gland around the anus, suggests that faeces may be impregnated with different odours at least between males and females. Mongoose latrine situation, near resting sites and inside core areas, suggests that faeces may be used as a self-recognition of the terrain, as territorial marking of core areas, which are exclusive among adult individuals of the same sex (PALOMARES and DELIBES 1993a), and to facilite communication among family group members (EWER 1973; GOSLING and MCKAY 1990).

DÜCKER (1965) remarked that Viverrinae usually use permanent latrines, whereas Herpestinae tend to switch their latrines often. ROEDER (1980a) pointed out that genets use permanent latrines, a spontaneous latrine switch being very rare. In this study these tendencies were observed in genets and mongooses, although for the former it was observed more sporadically than permanent latrines. The formation of temporal latrines seems different in each species. Roaming genets such as the radio-tracked male, could be the cause in this species. With mongooses, it could be mainly produced by a contagious defecation by some mongooses travelling together, a frequent event in Doñana (PALOMARES and DELIBES 1993a). This could be ascertained on several occasions in the Coto del Rey.

Even lacking detailed information, the mongoose behaviour observed in Doñana does not seem to coincide with that reported by BEN-YAACOV and YOM-TOV (1983) in Israel,

where mongooses appear to use permanent latrines. In Israel, mongooses seem to use permanent resting sites (BEN-YAACOV and YOM-TOV 1983), but in Doñana they often change resting sites (PALOMARES and DELIBES 1993b). Since mongooses tend to make latrines near resting sites, this behaviour might explain such differences. Also in Israel, BEN-YAACOV and YOM-TOV (1983) found scattered faeces, which were ascribed to roaming individuals.

Defecation sites used by genets in Doñana (mainly trees) have been little reported in other areas, where rocks are the commonest (e. g. LIVET and ROEDER 1987). However, this difference is probably because rocks are not available in Doñana. On the other hand, an interesting finding was the different faecal marking behaviour found between genets living in the Biological Reserve and Coto del Rey. Habitat composition in each area is different, and therefore this might be the reason for the differences. Variations in marking behaviour attributed to habitat changes are frequent in other carnivores (MACDONALD 1980; SMITH et al. 1989; DELIBES et al. 1991).

Two annual peaks in the number of faeces at latrines were observed in both species. Those of February–March for genets and January–February for mongooses could be due to mating, which takes place at these times (AYMERICH 1982; PALOMARES and DELIBES 1992). Moreover, an increase in marking behaviour and inspection of scent marking during the mating period has been observed in captive genets (ROEDER 1980a, 1980b), and tigers (SMITH et al. 1989). The peaks detected in November–December for genets and September–October for mongooses could be caused by the dispersal of young animals in the former (see MACDONALD and MASON 1987, for the otter, *Lutra lutra*), and because mongooses travel more often in family groups at that time (PALOMARES and DELIBES 1993a), there being more individuals able to deposit their faeces at the same sites.

Acknowledgements

The research was supported by DGICYT (project PB87-0405). The author had a postdoctoral grant of Consejo Superior de Investigaciones Científicas. C. DE LA COURT helped in the field work while searching for genet latrines in the Coto del Rey area. M. DELIBES, S. M. MACDONALD and an anonymous referee provided useful comments on an early draft of this manuscript. N. BUSTAMANTE reviewed the English version and C. KELLER translated the German summary.

Zusammenfassung

Markierung durch Defäkation bei freilebenden Ginsterkatzen, Genetta genetta, und Mangusten, Herpestes ichneumon, in Südwest-Spanien

Die Defäkationsgewohnheiten von Ginsterkatzen und Mangusten wurden im Nationalpark Doñana von November 1985 bis November 1989 studiert. Ginsterkatzen und Mangusten lagern ihren Kot oft in Latrinen ab. Als solche benutzen Ginsterkatzen Hohlstellen in Bäumen im Grenzbereich ihrer Habitate, während Mangusten ihren Kot am Boden ablagern und ihre Latrinen sich im Bereich des bevorzugten Habitats und in der Nähe von Schlafplätzen befinden. Ginsterkatzen markieren intensiver von Februar bis März und von November bis Dezember, und Mangusten von Januar bis Februar und September bis Oktober. Bei beiden Arten wird dieselbe Latrine von verschiedenen Individuen benutzt. Es scheint, daß Latrinen zum Informationsaustausch zwischen Individuen dienen.

References

AYMERICH, M. (1982): Contribution à l'étude de la biologie de la genette (*Genetta genetta* L.) en Espagne. Mammalia **46**, 389–393.

BAKER, C. M. (1988): Scent marking behaviour in captive water mongoose (*Atilax paludinosus*). Z. Säugetierkunde **53**, 358–364.

BEADER, S. K.; RANDALL, R. M. (1978): The use of fecal marking sites by spotted hyenas and civets. Carnivore **1**, 32–48.

BEN-YAACOV, R.; YOM-TOV, Y. (1983): On the biology of the Egyptian Mongoose, *Herpestes ichneumon*, in Israel. Z. Säugetierkunde **48**, 34–45.

Delibes, M.; Macdonald, S. M.; Mason, C. F. (1991): Marking activity in otters (*Lutra lutra*): a comparison between catchments in Andalucia and Wales. Mammalia **55**, 567–578.

Dücker, G. (1965): Das Verhalten der Schleichkatzen (Viverridae). Hb. Zool. (Berl.) **8**, 1–48.

Ewer, R. F. (1973): The Carnivores. New York. Cornell University Press.

Gorman, M. L.; Trowbridge, B. J. (1989): The role of odor in the social lives of carnivores. In: Carnivore behavior, ecology, and evolution. Ed. by: J. L. Gittleman. London: Chapman and Hall. Pp. 57–89.

Gosling, L. M. (1982): A reassessment of the function of scent marking in territories. Z. Tierpsychol. **60**, 89–118.

Gosling, L. M.; McKay, H. V. (1990): Competitor assessment by scat matching: an experimental test. Behav. Ecol. Sociobiol. **26**, 415–420.

Hefelz, A.; Ben-Yaacov, R.; Yom-Tov, Y. (1984): Sex specificity in the anal gland secretion of the Egyptian mongoose *(Herpestes ichneumon*. J. Zool. (London) **203**, 205–209.

Livet, F.; Roeder, J. J. (1987): Encyclopédie des carnivores de France. La genette (*Genetta genetta* Linnaeus, 1758). Soc. Franç. Etude Prot. Mamm. **17**, 1–33.

Macdonald, D. W. (1980): Patterns of scent marking with urine and faeces amongst carnivore communities. Symp. Zool. Soc. Lond. **45**, 107–139.

Macdonald, S. M.; Mason, C. F. (1987): Seasonal marking in an otter population. Acta Theriol. **32**, 449–462.

Moran, G.; Sorensen, L. (1986): Scent marking behaviour in a captive group of meerkats (*Suricata suricata*). J. Mammalogy **67**, 120–132.

Palomares, F.; Delibes, M. (1988): Time and space use by two common genets *(Genetta genetta)* in the Doñana National Park, Spain. J. Mammalogy **69**, 635–637.

— — (1990): Habitat preference of Large Grey mongoose, *Herpestes ichneumon*, in Spain. Acta Theriol. **35**, 1–6.

— — (1991a): Ecología comparada de la gineta *Genetta genetta* (L.) y el meloncillo *Herpestes ichneumon* (L.) (Mammalia, Viverridae) en Doñana (SO de la Península Ibérica). Bol. R. Soc. Esp. Hist. Nat. (Sec. Biol.) **87**, 257–266.

— — (1991b): Alimentación del meloncillo *Herpestes ichneumon* y de la gineta *Genetta genetta* en la Reserva Biológica de Doñana, S. O. de la Península Ibérica. Doñana Acta Vert. **18**, 5–20.

— — (1991c): Dieta del meloncillo, *Herpestes ichneumon*, en Coto del Rey, Norte del Parque Nacional de Doñana. Doñana Acta Vert. **18**, 187–194.

— — (1992): Some physical and population characteristics of Egyptian mongooses *Herpestes ichneumon* (L., 1758) in southwestern Spain. Z. Säugetierkunde **57**, 94–99.

— — (1993a): Social organization in the Egyptian mongoose: group size, spatial behaviour, and interindividual contacts in adults. Anim. Behav. **45** (in press).

— — (1993b): Resting ecology and behaviour of Egyptian mongooses in southwestern Spain. J. Zool (London) (in press).

Rasa, O. A. (1973): Marking behaviour and its social significance in the African dwarf mongoose, *Helogale undulata rufula*. Z. Tierpsychol. **32**, 293–318.

Roeder, J. J. (1980a): Les emplacements de defecations chez la genette *Genetta genetta* L. Rev. Ecol. (Terre Vie) **34**, 485–494.

— (1980b): Marking behaviour and olfactory recognition in genets (*Genetta genetta* L., Carnivora = Viverridae). Behaviour **72**, 200–210.

Smith, J. L. D.; McDougal, C.; Miquelle, D. (1989): Scent marking in free-ranging tigers, *Panthera tigris*. Anim. Behav. **37**, 1–10.

Author's address: Dr. Francisco Palomares, Estación Biológica Doñana, Consejo Superior de Investigaciones Científicas, Avda. Maria Luisa s/n, E-41013 Sevilla, Spain

Z. Säugetierkunde 58 (1993) 232–239
© 1993 Verlag Paul Parey, Hamburg und Berlin
ISSN 0044-3468

Karyological differences between two *Apodemus* species in Bulgaria

By RENA S. NADJAFOVA, NINA SH. BULATOVA, ZENKA CHASOVLIKAROVA, and S. GERASSIMOV

Severtzov Institute of Evolutionary Morphology and Ecology of Animals, Russian Academy of Sciences, Moscow; and Institute of Zoology, Bulgarian Academy of Sciences, Sofia

Receipt of Ms. 2. 9. 1992
Acceptance of Ms. 10. 11. 1992

Abstract

Described on the basis of a karyological study two cytotypes of Bulgarian wood mice (genus *Apodemus*, subgenus *Sylvaemus*) which differ completely in the distribution of their constitutive heterochromatin, the position of NOR as well as the pattern of G-banding in several autosomes and the X-chromosome. Their identification based on known European and Transcaucasian karyotypes was carried out. In addition to three previously described cytotypes in Transcaucasian mice, two cytotypes are distinguished in Bulgarian specimens. One of them apparently corresponds to *A. flavicollis* now absent in Transcaucasia. The other cytotype appears to belong to "*sylvaticus*" genomes by virtue of the large amounts of distal heterochromatic areas. Compared to some previously reported European examples of *A. sylvaticus*, here called "*sylvaticus*-E1", it was classified as "*sylvaticus*-E2" similar to an Austrian sample. The data obtained clearly contradict the generally accepted karyological conservatism of species of the genus *Apodemus*.

Introduction

Contrary to a widely spread opinion of karyological conservatism of 48-chromosome karyotypes in species of *Apodemus* (subgenus *Sylvaemus*), variability does exist but is revealed only after differential staining of chromosomes. Firstly, these differences concern heterochromatin distribution (ENGEL et al. 1973; BEKASOVA et al. 1980; GAMPERL et al. 1982; HIRNING et al. 1989) demonstrated mainly in European mice. Another important characteristic seems to be the localization of nucleolus organizer regions (NORs) on acrocentric chromosomes (HIRNING et al. 1989; BULATOVA et al. 1991).

Using these markers at least three cytotypes were recently found in Transcaucasus. All cytotypes or their combinations demonstrate sympatric distribution without any introgression in Azerbaijan (NADJAFOVA 1989). At the same time, absence of true *A. flavicollis* in this region was confirmed based on karyological evidence (KOZLOVSKY et al. 1990; BULATOVA et al. 1991).

Data obtained from karyological and parallel biochemical analyses (VORONTSOV et al. 1989; MEZHZHERIN 1990) have shed doubt on the widely held opinion of LARINA (1958) concerning hybridization of Transcaucasian wood (*A. sylvaticus*) and yellow-necked (*A. flavicollis*) mice in nature.

Due to overlapping of diagnostic morphological characters new biochemical criteria have been suggested which can be used for unambiguous determination of these species in southern Europe (BRITTON-DAVIDIAN et al. 1991).

To date, improved karyological techniques for revealing intrachromosomal differentiation have not been applied for the analysis of these populations. For the first time we obtained data from differential staining of chromosomes from individuals of *Apodemus* from Bulgaria and compared these with Transcaucasian samples previously identified.

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5804-0232 $ 02.50/0

Material and methods

Karyological analysis was carried out on samples of mice not yet identified to the species level which had been caught at three sites in Bulgaria, in the autumn of 1989 and in spring of 1990. Six individuals (5 ♂♂, 1 ♀) were caught in the mountain region of Stara Planina (near Karlukovo village, 100 km north-east from Sofia), 11 individuals (3 ♂♂, 8 ♀♀) on Vitosha mountain (village Lozen, vicinity of Sofia) and 4 individuals (2 ♂♂, 2 ♀♀) in the Thrace lowland (village Goleminovo, vicinity of Pazardjik).

During 1990–1991 all animals were karyotyped. The colour pecularities of the pelage, presence and shape of the chest spot and main body measurements were registered. The skulls of specimens are deposited in the laboratory of microevolution and domestication of mammals (head Prof. V. N. Orlov), Severtzov Institute of Evolutionary Morphology and Ecology of Animals.

Comparative karyological analysis of metaphase plates was performed using conventional methods. The technique used for NORs localization and identification of NOR-bearing chromosomes was described earlier (Bulatova et al. 1991).

Results

All studied animals except two from Lozen with additional chromosomes had the same diploid number common to all representatives of the genus *Apodemus*, i.e. 2n = 48. All chromosomes were acrocentric. Mice from Lozen and two individuals from Karlukovo had exclusively a centromeric localization of heterochromatin which was considered to be a specific feature of the cytotype *"flavicollis"* (Engel et al. 1973). All studied mice from Goleminovo and 4 ♂♂ from Karlukovo belong to the quite different cytotype, close to *"sylvaticus"* because of the almost exclusively telomeric localization of the heterochromatin (Engel et al. 1973; Gamperl et al. 1982). This cytotype was denoted as *"sylvaticus*-E2" for reasons discussed below.

The cytotype *"flavicollis"*

Among 13 examined animals 11 (3 ♂♂, 8 ♀♀) had a diploid chromosome number of 48 (Fig. 1a). In two individuals (♂ and ♀) from Lozen the diploid chromosome number varied in different cells from 48 to 51, obviously due to the presence of 1–3 additional chromosomes. These are small acrocentrics revealed among constant elements of the set by C- and G-patterns.

The X-chromosome is identified according to the G-banding as one of the largest chromosomes. Additional chromosomes are stained rather dark and without distinct G-bands (Fig. 1d).

Structural heterochromatin revealed when using C-staining is distributed almost uniformly throughout centromeric regions of all chromosomes of the basic set. Telomeric blocks were not found on any of the chromosomes (Fig. 1b). The Y-chromosome is rather large, with a length not less than half that of the X-chromosome, and completely heterochromatic (Fig. 1c). Generally, additional chromosomes are of smaller size and have a weaker intensity of C-staining compared with the Y-chromosome (Fig. 1b).

In the silver-stained metaphase preparations NORs are located exclusively in telomeric areas of autosomes (Fig. 1f). The maximum number of NOR-bearing chromosomes was 9 pairs. However, the majority of cells on a slide revealed fewer numbers of NORs which confirms the simultaneous functional activity of only part of the available nucleolus organizers. Moreover, NORs may be expressed on only one of two homologues of the same pair.

All individuals of this population had similar ochre colouring of back pelage. Most mice had a "collar"-shaped chest spot, one male being without a chest spot at all. Length of the body varied from 91.0 to 115.0 mm, most mice had damaged tails, so they couldnot be used for analysis. Foot length varied between 22.0–24.5 mm, and ear length between

15.4–19.0 mm. Both individuals with additional chromosomes had a round chest spot, and a rather large body as well as foot length.

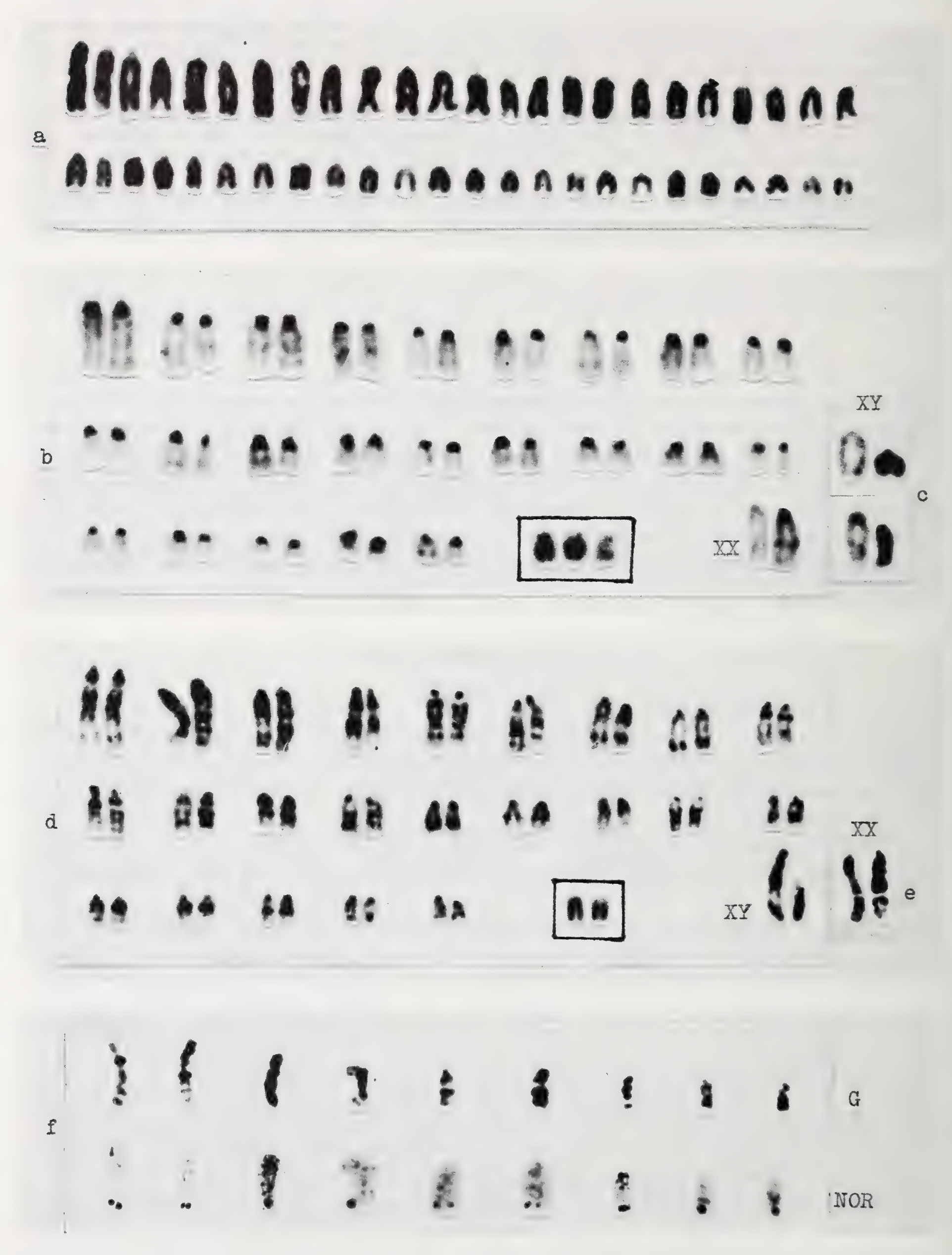


Fig. 1. Karyograms of *A. flavicollis* (Lozen): a: conventional staining by Giemsa (♀); b: C-banding (♀); c: Y-chromosome variants due to different level of spiralization; d: G-banding (♂); e: comparison of a G-banded X-chromosome of *A. sylvaticus* (right) and *A. flavicollis* (left); f: G-restaining of NOR-carrying autosomes from different karyograms. In outset = additional chromosomes



Fig. 2. Karyograms of *A. sylvaticus*: a: conventional staining by Giemsa (♀) (Goleminovo); b: C-banding (♀) (Goleminovo); c: C-banded gonosomes of a male (Goleminovo); d: G-banding (♂) (Karlukovo); e: G-banded X-chromosomes of a female (Goleminovo); f: G-restaining of NOR-carrying chromosomes from different karyograms

The cytotype "*sylvaticus*-E2"

The diploid number of chromosomes was found to be stable in the karyotypes of all studied animals (6 ♂♂, 2 ♀♀), 2n = 48, additional chromosomes were not found in any individuals (Fig. 2a).

Using G-staining all autosomes and X-chromosomes were identified (Fig. 2d). The pair of sex X-chromosomes of both females was heteromorphous in size and pecularities of differential staining. They have the same pattern of G-bands length-wise except for the pericentromeric region where the lengthy homologue has an additional dark G-band (Fig. 2e). It is worth noting that in the karyotypes of all examined males only the lesser homologue was found.

Compared with the above-described cytotype "*flavicollis*", distribution of heterochromatin in this cytotype is quite different. Heterochromatin is concentrated only in telomeric regions of small and medium-sized autosomes. Their number can attain 12 pairs. In the remainder of the autosomes heterochromatin was not found at all. On only some plates a small centromeric block and/or intercalaric band of heterochromatin was observed below the centromere in the largest autosome No. 1. Another pecularity of this cytotype seems to be the presence of a pronounced pericentromeric block of heterochromatin in the pair of large chromosomes of females, which corresponds to the X-chromosome identified by G-staining. Both homologues differ significantly by the amount of heterochromatic material (Fig. 2b). The Y-chromosome is medium-sized acrocentric and completely heterochromatic; the intensity of its staining corresponds to the staining of heterochromatic blocks of autosomes and the X-chromosome (Fig. 2c).

NORs were found to be located both in telomeric as well as centromeric areas of several chromosomes (Fig. 2f). It should be noted that the centromeric location occurs more rarely than the telomeric. On some plates centromeric NORs were not observed at all. Analysis of a large number of metaphases restained using different schemes (NOR-Giemsa, NOR-C, NOR-G) allowed us to conclude that NOR-bearing chromosomes belong to three different autosomal pairs. There were no more than 8 pairs of small and medium-sized chromosomes with a telomeric location of NORs. Similar to "*flavicollis*" studied here, NORs can be revealed either in both homologues of a pair or only in one.

Discussion

Traditionally in the fauna of Bulgaria two species of *Apodemus* – *A. sylvaticus* and *A. flavicollis* – can be recognized, taking into account combinations of some morphological and ecological pecularities. Reliability of assignment of each species depends on the sample size. Unambiguous individual identification of wood mice to the species level is ensured only when using genetic markers. Both sympatric and allopatric populations of Bulgarian *A. sylvaticus* and *A. flavicollis* can be differentiated clearly when using electrophoretic (Britton-Davidian et al. 1991) and karyological (our data) analyses.

So far, two cytotypes were described based on this material. One of these is undoubtedly characteristic for the true yellow-necked mouse, *A. flavicollis*. One pecularity of this cytotype is the centromeric location of the heterochromatin in all autosomes and the X-chromosome and another is the exclusively telomeric distribution of NOR (Engel et al. 1973; Gamperl et al. 1982; Hirning et al. 1989). Variations in the diploid chromosome number due to several additional, or B-chromosomes are possible in "*flavicollis*" cytotype (Wolf et al. 1972; Soldatovič et al. 1975; Král et al. 1979; Zima 1984; Sablina et al. 1985; Britton-Davidian et al. 1991).

C-stained karyotypes of *A. flavicollis* from Germany (Engel et al. 1973; Hirning et al. 1989), Austria (Gamperl et al. 1982) and the Leningrad region of Russia (Sablina et al.

1985) have been described. The localization of NORs has been studied in one German population near Ulm (HIRNING et al. 1989), and in the Ukraine, Estonia and Lithuania (BOESCOROV et al. 1990). According to these authors, the Y-chromosome was reported to be a medium-sized acrocentric, its size not being less than a half of the X-chromosome. Only in one Austrian population (Achenwald) was the Y-chromosome identified at the level of the smallest autosomes using conventional staining (KRÁL et al. 1979).

The second cytotype found in Bulgarian mice is characterized by a completely different distribution of heterochromatin and mixed (centromeric as well as telomeric) localization of NORs, as well as varying pattern of G-banding in several autosomes and the X-chromosome in comparison to *A. flavicollis* (Figs. 1d, e; 2d). In this type of chromosome set variability in the size of X-chromosomes at the expence of an increase or decrease in pericentromeric heterochromatin is observed. It should be noted that in two males of geographically rather distant populations (Goleminovo and Karlukovo) only one variant of a heteromorphous X-chromosome with relatively smaller content of heterochromatin was discovered.

The presence of telomeric heterochromatin is characteristic for the mice identified as *A. sylvaticus* by biochemistry and morphology. For the first time karyological pecularities of *A. sylvaticus* compared to *A. flavicollis* were described by ENGEL et al. (1973) according to their study of mice from Southern Germany (Freiburg).

Comparison of the data in the literature and our results confirms the existence of two cytotypes within European "*sylvaticus*", which we denoted as "*sylvaticus*-E1" and "*sylvaticus*-E2".

The "*sylvaticus*-E1" cytotype refers to mice earlier studied from Freiburg and the geographically close population of Ulm (Southern Germany). In the karyotype of these mice not more than 5 autosomal pairs were reported to carry telomeric blocks of heterochromatin. In addition, almost all chromosomes had centromeric heterochromatin. In the X-chromosome no centromeric heterochromatin has been revealed (ENGEL et al. 1973; HIRNING et al. 1989).

A. sylvaticus from Austria (GAMPERL et al. 1982) and from Bulgaria (our data) seem to be correspond to another cytotype "*sylvaticus*-E2". Karyotypes of these populations can be distinguished by the presence of centromeric heterochromatin in the only large pair of autosomes with varying heterochromatic block and by exclusive distribution of the remainder of heterochromatin in distal areas of several small and medium-sized chromosomes.

It is worth noting that the cytotype "*sylvaticus*-E2" does not seem to match any of the Transcaucasian karyotypic forms known to us (KOZLOVSKY et al. 1990; BULATOVA et al. 1991). At the same time some similarities in the heterochromatin and distribution of NORs could be seen in European "*sylvaticus*-E1" and the Azerbaijanian "t-form" (KOZLOVSKY et al. 1990).

We also failed to find the "*flavicollis*" cytotype in individuals of so-called "yellow-necked" mice from the Eastern Tanscaucasus although up to now the fauna of wood mice in this region has been considered to be represented by two species – *A. sylvaticus* and *A. flavicollis* – and by a number of mixed populations, presumably of hybrid origin (LARINA 1958).

The conclusion can be drawn that the species composition of mice in the regions of Transcaucasus and Balkans (particularly in Bulgaria) appears to have little in common.

In this connection we would like to emphasize that marked genetical (here cytogenetical) differences within the subgenus *Sylvaemus* are not unexpected. Indeed, in Europe the species *A. sylvaticus* is known to be highly differentiated both at the level of classical systematics and biochemical genetics (BERRY 1970; GEMMEKE 1980). At all, about two dozens subspecies were identified on European islands and in some regions of the continent, some of them superseding the species rank. It seems quite opportune to

reinvestigate their status on the basis of newly available approaches, among which the chromosome analysis seems to play an important role.

Unambiguous identification of *A. flavicollis* and complex *A. sylvaticus* cytotypes could be useful for clarifying species borderlines between their genomes. For example, additional chromosomes were reported by Zima (1984) for *A. sylvaticus* individuals. The critical examination of such cases is of both theoretical and practical interest.

Acknowledgements

We are grateful to Dr. Alexander Kozlovsky for helpful cytogenetic consultations in the course of this study. Russian authors were partly supported by the State Scientific-Technical Program "Perspective directions in genetics" during the phase of laboratory research.

Zusammenfassung

Chromosomenunterschiede zweier Apodemus-Arten in Bulgarien

Waldmäuse der Gattung *Apodemus* (Subgenus *Sylvaemus*) aus Bulgarien wurden karyologisch untersucht. Es wurden zwei Karyotypen gefunden, die sich grundsätzlich in der Menge des konstitutiven Heterochromatins, in der Lage der NOR-Regionen und im G-Bandenmuster verschiedener Autosomen und des X-Chromosoms unterscheiden. Beide wurden mit bereits bekannten Karyotypen aus Europa und Transkaukasien verglichen. Einer der bulgarischen Karyotypen scheint *A. flavicollis* zu repräsentieren, eine Art, die in Transkaukasien offenbar nicht vertreten ist. Der andere Karyotyp wird wegen seines großen Gehaltes an Heterochromatin *A. sylvaticus* zugeordnet. Diese Art ist karyologisch heteromorph und wird vorläufig in zwei Gruppen aufgeteilt: „*sylvaticus*-E1" (Süddeutschland) und „*sylvaticus*-E2" (Österreich, Bulgarien). Die Befunde zeigen, daß die Arten der Gattung *Apodemus* genetisch variabler sind als bisher angenommen.

Literature

Bekasova, T. S.; Vorontsov, N. N.; Korobitsyna, K. V.; Korablev, V. P. (1980): B-chromosomes and comparative karyology of the mice of the genus *Apodemus*. Genetica **52/53**, 33–43.

Berry, R. J. (1970): Covert and overt variation, as exemplified by British mouse populations. Symp. zool. Soc. Lond. **26**, 3–26.

Boescorov, G. G.; Lyapunova, E. A.; Belyanin, A. N.; Kartavtseva, I. V.; Zagorodnuk, I. V.; Zhezherina, T. O. (1990): Nucleolus organizing regions of wood mice chromosomes (*Apodemus* s. l.) as a diagnostic character. In: Evolutionary and genetical studies of mammals. Vol. 2. Ed. by T. Allenova et al. Vladivostok: DVO AN SSSR. Pp. 3–4 (in Russ.).

Britton-Davidian, J.; Vahdati, M.; Benmehdi, F.; Gros, P.; Nancé, V.; Croset, H.; Guerassimov, S.; Triantaphyllidis, C. (1991): Genetic differentiation in four species of *Apodemus* from Southern Europe: *A. sylvaticus, A. flavicollis, A. agrarius* and A. mystacinus (Muridae, Rodentia). Z. Säugetierkunde **56**, 25–33.

Bulatova, N. Sh.; Nadjafova, R. S.; Kozlovsky, A. I. (1991): Cytotaxonomic analysis of species of the genera *Mus Apodemus*, and *Rattus* in Azerbaijan. Z. zool. Syst. Evolut.-Forsch. **29**, 139–153.

Engel, W.; Vogel, W.; Voiculescu, L.; Rogers, H.; Zenzes, M. T.; Bender, K. (1973): Cytogenetic and biochemical differences between *Apodemus sylvaticus* and *Apodemus flavicollis* possibly responsible for the failure to interbreed. Comp. Physiol. and Biochem. **44B**, 1165–1173.

Gamperl, R.; Ehmann, Ch.; Bachmann, K. (1982): Genome size and heterochromatin variation in rodents. Genetica **58**, 199–212.

Gemmeke, J. (1980): Proteinvariation und Taxonomie in der Gattung *Apodemus* (Mammalia, Rodentia). Z. Säugetierkunde **45**, 348–365.

Hirning, U.; Schulz, W. A.; Just, W.; Adolph, S.; Vogel, W. (1989): A comparative study of the heterochromatin of *Apodemus sylvaticus* and *Apodemus flavicollis*. Chromosoma **98**, 450–455.

Kozlovsky, A. I.; Nadjafova, R. S.; Bulatova, N. Sh. (1990): Cytogenetical hiatus between sympatric forms of wood mice in Azerbaijan. Dokl. AN SSSR **315**, 219–222 (in Russ.).

Král, B.; Zima, J.; Herzig-Straschil, B.; Stěrba, O. (1979): Karyotypes of certain small mammals from Austria. Folia zool. (Brno) **28**, 5–11.

Larina, N. I. (1958): On problems concerning the diagnostics of closely related species – wood and yellow-necked mice. Zool. Zh. **37**, 1719–1732 (in Russ.).

MEZHZHERIN, S. V. (1990): Allozyme variability and genetic divergence of wood mice of subgenus *Sylvaemus* (Ognev et Vorobiev). Genetika (Moscow) **26**, 1046–1954 (in Russ.).
NADJAFOVA, R. S. (1989): Taxonomy and relationships of species of the family Muridae from Eastern Transcaucasia (Azerbaijan SSR). Unpubl. Thesis of Candidate dissertation. Moscow: Inst. Evol. Morphol. Ecol. Animals, USSR Acad. Sci. (in Russ.).
SABLINA, O. V.; RADJABLY, S. I.; GOLENISHCHEV, F. N. (1985): B-chromosomes in the karyotype of *Apodemus flavicollis* from the Leningrad district. Zool. Zh **64**, 1901–1902 (in Russ.).
SOLDATOVIĆ, B; SAVIČ, L.; SETH, P.; REICHSTEIN, H.; TOLKSDORF, M. (1975): Comparative study of the genus *Apodemus* Kaup, 1829. Acta Veterinaria (Beograd) **25**, 1–10.
VORONTSOV, N. N.; MEZHZHERIN, S. V.; BOESCOROV, G. G.; LYAPUNOVA, E. A. (1989): Genetical differentiation of sibling species of wood mice (*Apodemus*) in the Caucasus and their diagnostics. Dokl. AN SSSR **309**, 1234–1238 (in Russ.).
WOLF, U.; VOICULESCU, J.; ZENZES, M. T.; VOGEL, W.; ENGEL, W. (1972): Chromosome polymorphism in *Apodemus flavicollis* possibly due to a creation of a new centromere. In: Modern aspects of cytogenetics: Constitutive heterochromatin in man. Ed. by A. PFEIFFER. Stuttgart, New York: G. Fischer. Pp. 163–168.
ZIMA, J. (1984): Chromosomes of certain small mammals from southern Bohemia and the Šumava Mts. (ČSSR). Folia zool. (Brno) **33**, 133–141.

Author's addresses: Dr. RENA S. NADJAFOVA and Dr. NINA SH. BULATOVA, Severtzov Institute of Evolutionary Morphology and Ecology of Animals, Leninsky prospect 33, Moscow-117071, Russia; Prof. SVETOSLAV GERASSIMOV, ZENKA CHASOVLIKAROVA, Institute of Zoology, University of Sofia, bul. "Tsar Osvoboditel" 1, Sofia, Bulgaria

Z. Säugetierkunde 58 (1993) 240–243

ISSN 0044-3468

On the phylogeny of the genus *Acomys* (Mammalia: Rodentia)

By S. E. Fraguedakis-Tsolis, B. P. Chondropoulos, and N. P. Nikoletopoulos

Section of Animal Biology, Department of Biology, Patra University, Patra, Greece

Receipt of Ms. 1. 6. 1992
Acceptance of Ms. 2. 2. 1993

Abstract

Studied the phylogenetic relationships of the genus *Acomys* (represented by *A. minous*) to other rodent genera of the families Muridae and Arvicolidae (represented by *Mus domesticus, Rattus norvegicus, Apodemus flavicollis*, and *Microtus* (*Terricola*) *thomasi*, respectively). A total of 51 adult individuals of both sexes were used to determine the albumin differentiation by means of the microcomplement fixation test (MC'F). The immunological distances of *Acomys* from the murid taxa were found to be greater than that of the *Microtus* (*T.*) *thomasi* to the murid species tested. This means that the *Acomys* evolutionary lineage splitted off earlier than the appearence of the common ancestor of murids and arvicolids, at a time of 22–27 million years before present. Consequently, although the morphological and karyological data have suggested so far that the taxonomic position of *Acomys* is within the family Muridae, our immunological results indicate that the systematics of this genus should be reconsidered.

Introduction

The spiny mouse of Crete is a little known rodent of the Greek fauna the taxonomic position of which (at specific and subspecific level) is a matter of controversy since its first description. A review of this controversy is presented by Trichas (1988).

Accepting the more recent opinions on the systematics of this taxon (Matthey 1963; Dieterlen 1978) we consider it as a full species, *Acomys minous*, endemic of Crete as it was proposed at first by Bate (1913). Furthermore, the taxonomic status of the genus *Acomys* among the other rodent genera is also unclear. Traditionally, *Acomys* is classified within the family Muridae on the basis of morphological and chromosomal data (Zimmermann 1953; Zahavi and Wahrman 1956; Dieterlen 1963, 1978; Matthey 1963; Matthey and Baccar 1967; Baccar 1969) but electrophoretic and immunological data make this very doubtful (Bonhomme et al. 1985; Sarich 1985). Since this problem is not satisfactorily solved so far we have undertaken to study the phylogenetic relationships of *Acomys* not only in comparison with murid rodents but also to rodents of the family Arvicolidae.

The analysis of the phylogenetic relationships among the studied taxa has been carried out by the definition of their albumin differentiation using the microcomplement fixation method (MC'F).

Materials and method

A total of 51 individuals of the species *Mus domesticus, Rattus norvegicus, Apodemus flavicollis*, of the family Muridae, and the species *Microtus* (*Terricola*) *thomasi* of the family Arvicolidae were trapped alive at five localities of the Greek mainland. Also 4 individuals of the *Acomys minous* originating from two localities of Crete were used. Trapping localities and the number of individuals of each species studied are shown in table 1.

The procedure of blood sampling, albumin isolation, antisera preparation and MC'F experiments have been described previously (Nikoletopoulos et al. 1992).

The average immunological distances between the studied taxa resulting from the MC'F experiments were used for the construction of an evolutionary tree according to the Fitch and Margoliash (1967) method. Prager and Wilson (1978) emphasize that this method is the most reasonable to use for constructing phylogenetic trees on the basis of immunological data.

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5804-0240 $ 02.50/0

Table 1. **Number of individuals of the studied taxa and trapping localities in Greece**

Species	Number of individuals	Trapping locality
Mus domesticus	21	Patra University Campus, Achaia Pref., Peloponnese
Apodemus flavicollis	12	Kastritsi, Achaia Pref., Peloponnese
Rattus norvegicus	4	Patra University Campus, Achaia Pref., Peloponnese
Microtus (Terricola) thomasi	14	Itea, Fokida Pref., Central Greece
Acomys minous	4	Agios Nikolaos and Sitia, Lasithi Pref., Crete

Results and discussion

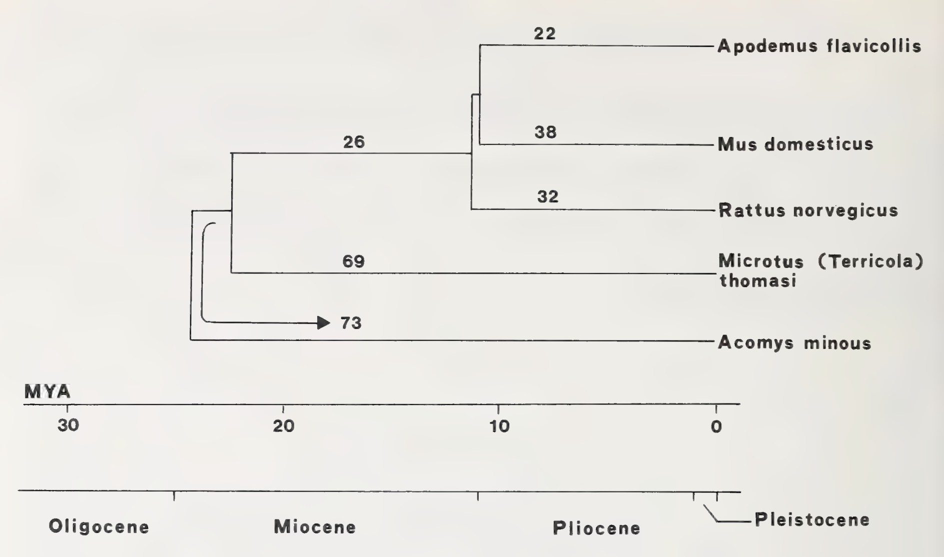
The results of reciprocal MC'F tests concerning the albumin of five species to which antibodies were prepared are given in table 2. The reliability of immunological data for estimating amino acid sequence divergence between proteins is, in part, proportional to the percent standard deviation from reciprocity for two way comparisons (Beverley and Wilson 1982). The standard deviation value derived from our experiments was found to be 7.1; such a value lies within the range reported for similar studies (Ellis and Maxson 1980; Fuller et al. 1984; Nikoletopoulos et al. 1992).

Table 2. **Matrix of reciprocal immunological distances (I.D. units) of the studied rodent albumins**

Species	Immunological distance Antisera against				
	M. d.	*A. f.*	*R. n.*	*M. (T.) t.*	*A. m.*
Mus domesticus (M. d.)	0	57	61	152	116
Apodemus flavicollis (A. f.)	63	0	61	118	123
Rattus norvegicus (R. n.)	65	61	0	136	166
Microtus (T.) thomasi (M. [T.] t.)	132	102	118	0	136
Acomys minous (A. m.)	140	98	138	147	0

The phylogenetic tree (Figure) was constructed using the average reciprocal values of the albumin immunological distances. The statistical evaluation of the goodness of fit of this tree to the input data is expressed by either the percent standard deviation (s) (Fitch and Margoliash 1967) or the percent error (F) (Prager and Wilson 1976). In our tree these values are s = 8.5 and F = 6.5. Comparable values are mentioned in other phylogenetic studies based on the same technique (see Nikoletopoulos et al. 1992).

As is already known (Sarich 1985; Nikoletopoulos et al. 1992) the rate of albumin evolution is faster in rodents than in other mammalian groups. Nikoletopoulos et al. (1992) discussed this subject and proposed a rate equal to 100 amino acid substitutions per 16–20 million years, according to the correlation of the available immunological and paleontological data on rodents. On the basis of this rate the results of the present study indicate that the *Acomys* lineage branched off 22–27 million years ago (MYA), during the late Oligocene – early Miocene period. On the other hand the Muridae-Arvicolidae divergence seems to have taken place 20–25 MYA (early Miocene), as becomes clear from



Phylogenetic tree of the five rodent taxa constructed on the basis of the average albumin immunological distances. The numbers on the branches show the amount of albumin changes estimated to have occurred along each branch

our results. Thus it is apparent that the genus *Acomys* is phylogenetically more distant from the examined taxa of Muridae than that of Arvicolidae, a fact that is also supported by SARICH (1985) who has wondered if *Acomys* is really a murine or even a murid.

Because of the remarkable scarcity of the *Acomys* fossil records, the age of the genus is difficult to determine on the basis of paleontological data. Information on the divergence time of this taxon is given by MATTHEY (1963, 1968), who accepts the existance of *Acomys* in Asian areas during the Miocene period. He also suggests that this genus was therefrom distributed to the Near East, Africa, Crete and Cyprus during the upper Pliocene and early Pleistocene period. DENYS (1990) summarizing his own and bibliographic data concludes that the divergence time of *Acomys* is between 11 and 5 MYA; however he cannot give a definitive answer to the question whether *Acomys* is a true murid or not.

To date there is no information about the occurrence of *Acomys* in the Miocene strata. However, JACOBS (1977) suggests that the oldest known murid fossils (*Antemus*) is of a middle Miocene age (15–16 MYA). If our and SARICH's (1985) immunological results are accepted then the phylogenetic position of *Acomys* should not be within the family Muridae, although even some contemporary authors based on morphological and karyological data continue to consider that *Acomys* is a genus of Muridae (NEVO 1985; DIPPENAAR and RAUTENBACH 1986).

Acknowledgements

We are grateful to Dr. A. LEGAKIS and his colleagues (University of Crete) who supplied us with the *Acomys* individuals.

Zusammenfassung

Über die Phylogenie der Gattung Acomys (Mammalia: Rodentia)

Die phylogenetischen Beziehungen der Gattung *Acomys* (vertreten durch *A. minous*) zu anderen Rodentia-Gattungen der Familien Muridae (vertreten durch *Mus domesticus, Rattus norvegicus, Apodemus flavicollis*) und Arvicolidae (vertreten durch *Microtus* (*Terricola*) *thomasi*) werden untersucht. Insgesamt 51 erwachsene Individuen beider Geschlechter wurden untersucht, um die Albumin-

Differenzierung durch den Microcomplement-Fixations-Test (MC'F) klarzustellen. Die immunologischen Abstände von *Acomys* von den Muriden-Taxa erwiesen sich als größer im Vergleich zu den entsprechenden Abständen zwischen *Microtus* (*T.*) *thomasi* und den untersuchten Muriden-Arten. Das bedeutet, daß die Abzweigung der Evolutionslinie zu *Acomys* älter ist als das Auftauchen des gemeinsamen Vorfahren der Muriden und Arvicoliden – etwa vor 22–27 Mio. Jahren. Den immunologischen Ergebnissen zufolge sollte die taxonomische Stellung von *Acomys* innerhalb der Familie Muridae – im Gegensatz zu den bisherigen morphologischen und karyologischen Daten – revidiert werden.

References

BACCAR, H. (1969): Contribution à la cytogénétique des Muridae du genre *Acomys* Geoffroy. Montreux, Imp. Ganguin et Laubscher. Th-Sc., Lausanne.

BEVERLEY, S. M.; WILSON, A. C. (1982): Molecular evolution in *Drosophila* and higher Diptera. I. Micro-complement fixation studies of a larval hemolymph protein. J. Molec. Evol. **18**, 251–264.

BONHOMME, F.; ISKANDAR, D.; THALER, L.; PETTER, F. (1985): Electromorphs and phylogeny in muroid rodents. In: Evolutionary relationships among rodents, a multidisciplinary analysis. Ed. by W. P. LUCKETT and J.-L. HARTENBERGER. New York: Plenum Press. Series A: Life Sciences, Vol. **92**, 671–683.

DENYS, C. (1990): The oldest *Acomys* (Rodentia, Muridae) from the Lower Pliocene of South Africa and the problem of its murid affinities. Palaeontographica (Abt. A) **210**, 79–91.

DIETERLEN, F. (1963): Zur Kenntnis der Kreta-Stachelmaus, *Acomys* (*cahirinus*) *minous* Bate. Z. Säugetierkunde **28**, 47–57.

— (1978): *Acomys minous* (Bate, 1905). – Kreta-Stachelmaus. In: Handbuch der Säugetiere Europas. Ed. by J. NIETHAMMER and F. KRAPP. Wiesbaden: Akad. Verlagsges. Vol. **1/I**, 452–461.

DIPPENAAR, N. J.; RAUTENBACH, I. L. (1986): Morphometrics and karyology of the southern African species of the genus *Acomys* I. Geoffroy Saint-Hilaire, 1838 (Rodentia, Muridae). Ann. Transvaal Mus. **34**, 129–183.

ELLIS, L. S.; MAXSON, L. R. (1980): Albumin evolution within New World squirrels (Sciuridae). Amer. Midl. Nat. **104**, 57–62.

FITCH, W. M.; MARGOLIASH, E. (1967): Construction of phylogenetic trees. Science **155**, 279–284.

FULLER, B.; LEE, M. R.; MAXSON, L. R. (1984): Albumin evolution in *Peromyscus* and *Sigmodon*. J. Mammalogy **65**, 466–473.

JACOBS, L. L. (1977): A new genus of Murid rodent from the Miocene of Pakistan and comments on the origin of the Muridae. Paleo-bios. **25**, 1–11.

MATTHEY, R. (1963): Polymorphisme chromosomique intraspecifique et intraindividuel chez *Acomys minous* Bate (Mammalia-Rodentia-Muridae). Chromosoma **14**, 468–497.

— (1968): Cytogénétique et taxonomie du genre *Acomys. A. percivalli* Dollman et *A. wilsoni* Thomas, espèces d'Abyssinie. Mammalia **32**, 621–627.

MATTHEY, R.; BACCAR, H. (1967): La formule chromosomique d'*Acomys seurati* H. de B. et la cytogénétique des *Acomys* paléarctiques. Rev. suisse Zool. **74**, 546.

NEVO, E. (1985): Genetic differentiation and speciation in spiny mice, *Acomys*. Acta Zool. Fennica **170**, 131–136.

NIKOLETOPOULOS, N. P.; CHONDROPOULOS, B. P.; FRAGUEDAKIS-TSOLIS, S. E. (1992): Albumin evolution and phylogenetic relationships among Greek rodents of the families Arvicolidae and Muridae. J. Zool. **228**, 445–453.

PRAGER, E. M.; WILSON, A. C. (1976): Congruency of phylogenies derived from different proteins. J. Molec. Evol. **9**, 45–57.

— — (1978): Construction of phylogenetic trees for proteins and nucleic acids: Empirical evaluation of alternative matrix methods. J. Molec. Evol. **11**, 129–142.

SARICH, V. M. (1985): Rodent macromolecular systematics. In: Evolutionary relationships among rodents, a multidisciplinary analysis. Ed. by W. P. LUCKETT and J.-L. HARTENBERGER. New York: Plenum Press. Series A: Life Sciences, Vol. **92**, 423–452.

TRICHAS, A. (1988): A first review on the insular endemic Spiny Mouse of Crete *Acomys minous* (Rodentia: Murinae). Rapp. Comm. int. Mer Mèdit. **31**, 131.

ZAHAVI, A.; WAHRMAN, J. (1956): Chromosome races in the genus *Acomys* (Rodentia: Murinae). Bull. Res. Counc. Israel **5B**, 316.

ZIMMERMANN, K. (1953): Die Rodentia Kretas. Z. Säugetierkunde **17**, 21–51.

Authors' address: S. E. FRAGUEDAKIS-TSOLIS, B. P. CHONDROPOULOS, and N. P. NIKOLETOPOULOS, Section of Animal Biology, Department of Biology, University of Patra, GR-26001 Patra, Greece

Z. Säugetierkunde 58 (1993) 244–251

ISSN 0044-3468

A major satellite DNA from the South American rodents of the genus *Ctenomys*

Quantitative and qualitative differences in species with different geographic distribution

By María Susana Rossi, O. A. Reig, and J. Zorzópulos

Grupo de Investigaciones en Biología Evolutiva, Departamento de Ciencias Biológicas and Departamento de Química Biológica, Facultad de Ciencias Exactas y Naturales, Unversidad de Buenos Aires, Buenos Aires, Argentina

Receipt of Ms. 31. 8. 1992
Acceptance of Ms. 7. 2. 1993

Abstract

The quantity and quality of the major satellite DNA present in South American rodents of the genus *Ctenomys* were analyzed in various species of the genus. The quantity was analyzed by genomic DNA hybridization with sequences of this major satellite DNA, in a dot-blot experiment. The quality was analyzed by hybridization of genomic DNA digested with restriction endonucleases, with sequences of this major satellite DNA, as well, in Southern-blot experimens. Quantitative and qualitative analyses were correlated with the geographic distribution of these species.

According to the dot-blot analysis performed under high-stringency conditions, *Ctenomys* species were classified in three groups containing none, low, and high amounts of this *Ctenomys* satelite DNA, respectively. The first group comprises only *C. opimus*. The second group comprises *C.* cf. *perrensi, C. tuconax*, and *C. occultus*. The last group includes *C. mendocinus, C. porteousi, C. azarae, C. australis*, and *C. talarum. C. latro* appears closely related to this last group but it shows some differences on its own. According to the quality of satellite *Ctenomys* DNA, *Ctenomys* species belonging to the last group are closely related, and all but one have a distinctive geographic distribution south of the 30°S latitude. In contrast, species of the second group seem to be more distantly related and all were found north of the 30°S latitude, as is also the case for *C. opimus*.

Introduction

A significant amount of the eucaryotic genome is composed of highly repetitive DNA sequences which are arranged tandemly over long stretches of DNA (Burtlag 1980). Common to most satellites are minor sequence variations between different repeat units, which in several cases have been shown to be clustered in segments of the satellite DNA (Hörz and Zachau 1977; Cooke and McKay 1978; Beauchamp et al. 1979). It is believed that the generation of these segments has involved independent amplification steps of single repeat units through a rolling-circle replication mechanism (Walsh 1987; Rossi et al. 1990). This particular replication mode may explain the significant variations observed in the satellite restriction patterns between animal species without extensive divergence in the overall repetitive sequence itself (Arnason 1982; Widegren et al. 1985; Bogenberger et al. 1987; Arnason et al. 1988; Rossi et al. 1990). Furthermore, random differences in the length of the segments generated during the satellite amplification may also result in large differences in the total amount of repetitive DNA of different species. Therefore, genomic DNA hybridization analysis before and after DNA digestion with restriction endonucleases, using as probe satellite DNA sequences (dot-blot and Southern-blot, respectively) to evaluate quantity and quality of satellite DNA, should result in valuable information on common ancestry of related groups.

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5804-0244 $ 02.50/0

Recently, a major satellite from the South American rodents of the genus *Ctenomys*, named RPCS (repetitive PvuII *Ctenomys* sequence), was described (Rossi et al. 1990). In the present study, the quantity and quality of this satellite DNA were investigated in several *Ctenomys* species by using both, dot-blot and Southern-blot analysis, respectively.

Material and methods

Specimens

We studied the DNA of an individual from each of 10 species of *Ctenomys*. All specimens were collected in the wild employing live traps. Skin and skull voucher specimens of all of them were deposited in the Collection of Mammals of the Municipal Museum of Natural History of Mar del Plata, Argentina. Geographic localities of the collected specimens, all from Argentina, are as follows (t.l. = type locality): *Ctenomys azarae* (Luan Toro, La Pampa), *Ctenomys australis* (Necochea, Buenos Aires, t.l.), *Ctenomys latro* (Tapia, Tucumán, t.l.), *Ctenomys talarum recessus* (Necochea, Buenos Aires), *Ctenomys tuconax* (El Infiernillo, Tucumán), *Ctenomys occultus* (Monteagudo, Tucumán, t.l.), *Ctenomys* cf. *perrensi* (2n = 54) (Saladas, Corrientes), *Ctenomys porteousi* (Bonifacio, Buenos Aires, t.l.), *Ctenomys mendocinus* (Tupungato, Mendoza), and *C. opimus* (Tres Cruces, Jujuy).

DNA extraction, enzyme digestion, and gels

DNA was extracted as described elsewhere (Rossi et al. 1990). The DNA was digested with restriction endonucleases (Bethesda Research Laboratories) according to the instructions of the manufacturer. The DNA fragments were separated in 1.2 % agarose gels (Maniatis et al. 1982).

Blotting and hybridization

For Southern-blot analysis, agarose gels were denatured, neutralized, and transferred nylon membranes (Pall Byodine), according to the method described by Southern (1975). For dot-blot analysis, DNA was denatured in 0.2 N NaOH, 10× standard saline citrate (SSC) (1× SSC = 0.15 M NaCl, 0.015 M trisodium citrate, pH 7) during 30 minutes at room temperature, and spotted onto the nylon membrane.

In both cases, prehybridization and hybridization were performed in a solution containing 6× SSC, 100 μg of salmon DNA (Sigma, USA)/ml, 0.5 % SDS and 0.3 % nonfat dry milk, and labeled DNA probe was hybridized with the DNA immobilized on the membranes for 18 h at 60 °C. Then the membranes were washed five times at 65 °C in 0.1× SSC (high stringency) and 1 % SDS. Hybrid DNA was detected by autoradiography, using 3M X-ray films and DuPont Lightening Plus screens.

Labeling of DNA

The RPCS probe was labeled radioactively to a specific activity of 10^8 cpm/μg by using the nick translation procedure (Rigby et al. 1977).

Isolation and cloning of the satellite DNA

The isolation, cloning, and characterization of the monomer of the major satellite DNA of *Ctenomys* (RPCS), as well as its nucleotide sequence, were described elsewhere (Rossi et al. 1990).

Results

Relative amounts of the major satellite DNA in several *Ctenomys* species

The monomer of the major satellite DNA of *Ctenomys*, RPCS, is 337 base pairs long, and ~ 42 % C+G (Rossi et al. 1990). This monomer was originally cloned from *Ctenomys porteousi*, and we estimate that this species has ~ 3×10^6 copies of the monomer per haploid genome.

Genomic DNA was isolated from liver of several species of *Ctenomys*. Equal amounts

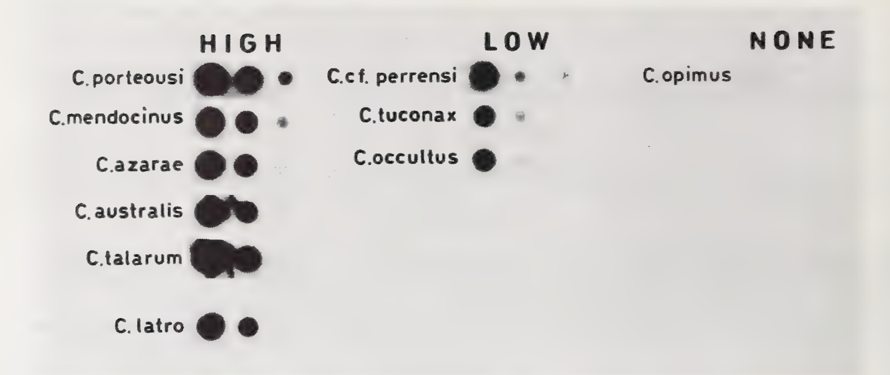


Fig. 1. Quantitative analysis of RPCS in different *Ctenomys* species by dot-blot experiment. Hybridization to labeled RPCS was performed under high-stringency conditions. In all cases the amounts of DNA were 1000, 100, and 10 ng

of these DNAs were spotted on nylon membranes and hybridizated to labeled RPCS (dot-blot technique). The hybridization was carried out under conditions where 95 % identity would be expected to generate a signal. Hybridization was positive for every spot containing *Ctenomys* DNA, except in the one containing *Ctenomys opimus* DNA (Fig. 1). According to these results, the species of *Ctenomys* were classified into three major groups (Table).

Classes of *Ctenomys* species according to its content of RPCS

The amount of RPCS was estimated by dot-blot hybridization performed under high-stringency conditions (see Fig. 1)

High	Low	None
C. porteousi	*C.* cf. *perrensi*	*C. opimus*
C. mendocinus	*C. tuconax*	
C. azarae	*C. occultus*	
C. australis		
C. talarum		
C. latro		

Qualitative analysis of the RPCS satellite in several *Ctenomys* species

Figure 2 shows several restriction endonucleases hybridization patterns of RPCS satellite sequences present in several *Ctenomys* species. The restriction endonucleases employed were EcoR I, Pst I, Hinf I, and Ava II.

As previously reported (Rossi et al. 1990), these patterns demonstrate the existence of interspecies differences in the proportion of monomers of RPCS with restriction sites for different restriction endonucleases. However, the patterns corresponding to RPCS sequences present in *C. porteousi, C. australis, C. azarae, C. mendocinus*, and *C. talarum* were identical, while *C. latro* presented some differences, mainly in the EcoR I and Pst I patterns. This group of species is the same which results from the quantitative analysis of figure 1, as the one with high content of RPCS.

In contrast, the species of the group containing low amounts of RPCS possess different restriction patterns. Furthermore, these patterns are clearly different from the restriction patterns of the species belonging to the group with high content of RPCS.

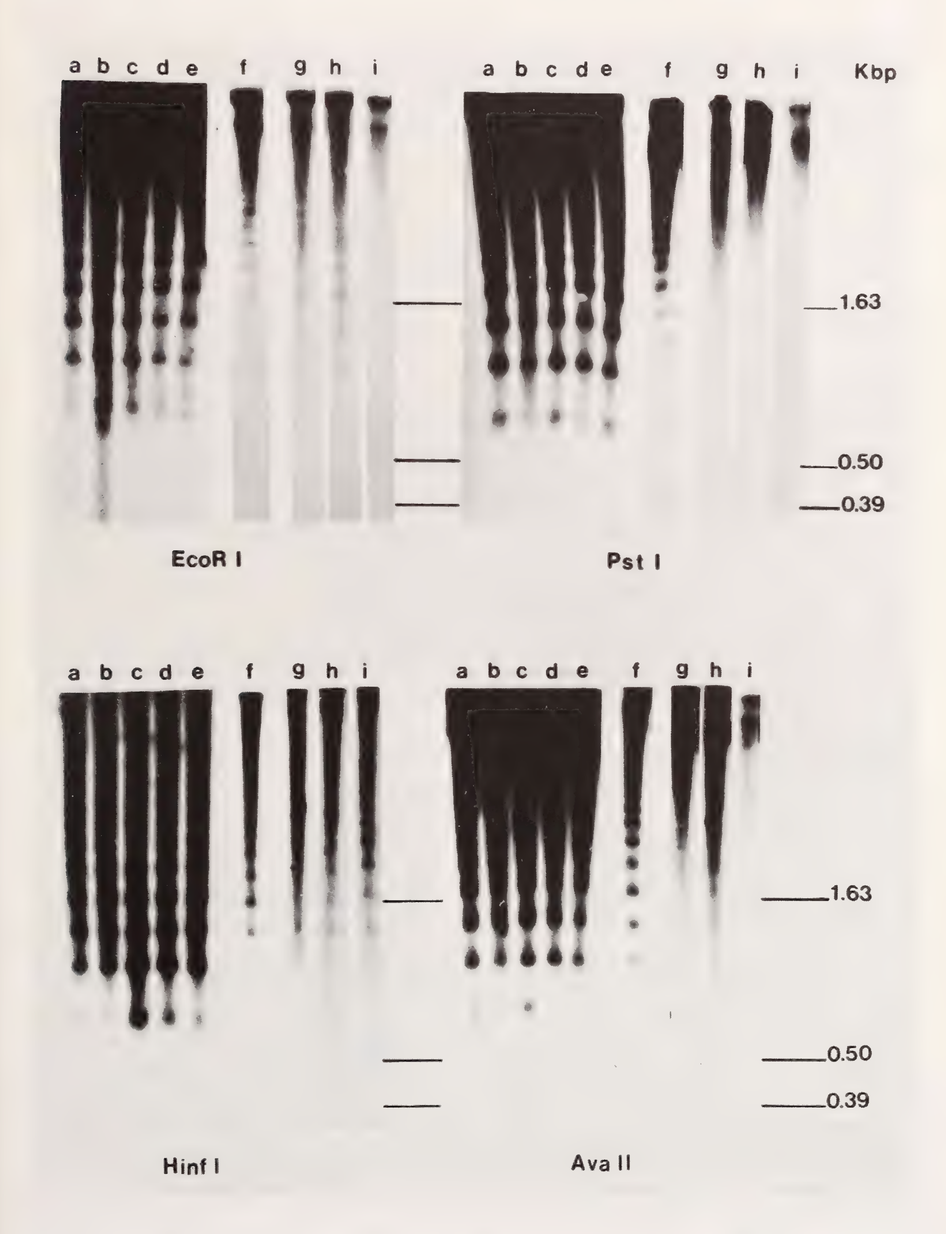


Fig. 2. Qualitative analysis of RPCS in different species of *Ctenomys* by Southern-blot experiments. The genomic DNAs were cleaved with EcoR I, Pst I, Hinf I, and Ava II. Hybridization to labeled RPCS was performed under high-stringency conditions. a: *C. mendocinus*, b: *C. porteousi*, c: *C. australis*, d: *C. talarum*, e: *C. azarae*, f: *C. latro*, g: *C.* cf. *perrensi* (2n = 54), h: *C. tuconax*, and i: *C. occultus*

Correlation between geographic distribution and the quantity and quality of RPCS in the studied species of *Ctenomys*

Figure 3 shows the geographic distribution of the *Ctenomys* species here studied. It can be observed that species containing high amounts of RPCS and a typical satellite restriction pattern described above also have a distinctive geographic distribution. All of them, with the exception of *C. latro*, are distributed south of the 30°S latitude. North of this latitude all the members of the group are distributed containing low amounts of RPCS and also *C. opimus*, the only member of the group whose DNA does not cross-hybridize with the RPCS under high-stringency conditions.

Discussion

Rodents of the genus *Ctenomys* are members of the family Octodontidae, which occur in the southern cone of south America. *Ctenomys* is included in the subfamily Ctenomyinae (Reig 1986; Reig et al. 1990), characterized by advanced adaptations to a herbivorous subterranean life. A major satellite DNA present in members of the genus *Ctenomys*, whose monomer was named RPCS, was recently described (Rossi et al. 1990).

In the present work members of the genus *Ctenomys* were classified in three major groups according to their contents of RPCS measured by quantitative analysis performed under high-stringency conditions. In this conditions, *C. opimus* was the only species of the genus analyzed that gave a negative result. RPCS-related sequences were only detected in this species under relaxed hybridization conditions, and the Pvu II pattern for this *Ctenomys* species was also very different from the Pvu II pattern observed in other species of *Ctenomys* (see also Rossi et al. 1990).

A second group includes the species *C.* cf. *perrensi, C. tuconax*, and *C. occultus*. This group is characterized by its relative low content in RPCS. However, the species of this group are heterogeneous according to qualitative analysis of RPCS satellite DNA (Fig. 2) and show different karyotypes (Reig and Kiblisky 1969; Ortells et al. 1991).

The third group contains the species *C. porteousi, C. australis, C. azarae, C. mendocinus*, and *C. talarum*. These species are very homogeneous according to qualitative analysis (Fig. 2). They also share the same 2n = 48 diploid number. However, *C. talarum* differs from the remaining in G- and C-banding patterns (Massarini et al. 1991). *C. porteousi, C. australis, C. azarae*, and *C. mendocinus* have been clumped together in the *mendocinus* group because of their sharing very similar banding patterns and the presence of heterochromatin in full arm blocks (Massarini et al. 1991). We also include in this third group *C. latro*, which shows some minor differences in the qualitative analysis as compared to the former species. It also has a different 2n = 42 karyotype and a symmetrical sperm type.

All the species included in the third group with the exception of *C. latro* are distributed south of the 30°S latitude. North of this latitude are distributed all the members of the group containing low amounts of RPCS and also *C. latro* and *C. opimus*. This suggests that *C. latro* may be in some way related to a stock which colonized the southern part of Argentina and that most (if not all) of the living species located in this area are derived from this stock.

The correlation between geographic distribution and quantity and quality of the RPCS – with the exception of *C. latro* above discussed – is in agreement with the previous described correlation between sperm morphology and geographic location (Feito and Gallardo 1982; Vitullo et al. 1988; Vitullo and Cook 1991). For that reason there is the hope that the RPCS periodicities may afford valuable clues to understand the evolution of *Ctenomys*.



Fig. 3. Geographic distribution of the *Ctenomys* species studied in this work. The shady area denotes geographic distribution of the family Ctenomyidae according to VITULLO et al. (1988). ●, ◒, and ○ denote high, low and none content of RPCS, respectively, according to the quantitative analysis performed under high-stringency conditions. In parenthesis are included the type of sperm and the diploid number. S = symmetrical sperm, A = asymmetrical sperm

Acknowledgements

This paper is dedicated to the memory of Professor Osvaldo A. Reig, who died in Buenos Aires in March 1992.

Zusammenfassung

Eine bedeutende Satelliten-DNA von südamerikanischen Nagetieren der Gattung Ctenomys. Quantitative und qualitative Unterschiede von Arten mit verschiedener geographischer Verbreitung

Quantität und Qualität einer bedeutenden Satelliten-DNA wurden bei mehreren Arten südamerikanischer Nagetiere der Gattung *Ctenomys* untersucht. Die Quantität wurde mittels genomischer DNA-Hybridisations-Analyse mit Sequenzen dieser bedeutenden Satelliten-DNA in einem dot-blot Experiment, die Qualität mittels genomischer DNA-Hybridisations-Analyse nach Verdauung mit Restriktions-Endonukleasen, mit Sequenzen dieser bedeutenden Satelliten-DNA in einem Southern-blot Experiment, untersucht. Die quantitative und qualitative Analyse wurde mit der geographischen Verbreitung dieser Arten in Zusammenhang gebracht.

Nach der unter hohen Stranghybridisations-Bedingungen vorgenommenen dot-blot Analyse, werden die *Ctenomys*-Arten in 3 Gruppen gestellt, je nachdem, ob sie gar kein, wenig oder viel dieser *Ctenomys*-Satelliten-DNA enthalten. Die erste Gruppe enthält nur *C. opimus*. Die zweite Gruppe enthält *C.* cf. *perrensi, C. tuconax* und *C. occultus*. Die dritte Gruppe enthält *C. mendocinus, C. porteousi, C. azarae, C. australis* und *C. talarum*. *C. latro* scheint nah verwandt mit dieser letzten Gruppe zu sein, zeigt aber eigene Unterschiede. Je nach der Qualität dieser *Ctenomys*-Satelliten-DNA, sind die *Ctenomys*-Arten der dritten Gruppe nah miteinander verwandt und alle, außer einer, haben eine bestimmte geographische Verbreitung südlich des 30. Breitengrades. Im Gegensatz dazu scheinen die Arten der zweiten Gruppe entfernter verwandt zu sein und befinden sich alle nördlich des 30. Breitengrades. Das gleiche gilt für *C. opimus*.

References

Arnason, U. (1982): Southern blot hybridizations in cetaceans, using killer whale restriction fragment as a probe. Hereditas **97**, 47–49.

Arnason, U.; Allderdice, P. W.; Lien, J.; Widegren, B. (1988): Highly repetitive DNA in the baleen whale genera *Balaenoptera* and *Megapera*. J. Mol. Evol. **27**, 217–221.

Beauchamp, R. S.; Michell, A. R.; Buckland, R. A.; Bostock, C. J. (1979): Specific arrangements of human satellite III DNA sequences in human chromosomes. Chromosoma **71**, 153–166.

Bogenberger, J. M.; Neitzel, N.; Fitter, F. (1987): A highly repetitive DNA component common to all Cervidae: its organization and chromosomal distribution during evolution. Chromosoma **95**, 154–161.

Burtlag, D. L. (1980): Molecular arrangement and evolution of heterochromatic DNA. Ann. Rev. Genet. **14**, 121–144.

Cooke, H. J.; McKay, R. D. G. (1978): Evolution of a human Y-chromosome specific repeated sequences. Cell **13**, 453–460.

Dennis, E. S.; Dunsmuir, P.; Peacock, W. J. (1980): Segmental amplification in a satellite DNA: Restriction enzyme analysis of the major satellite of *Macropus rufogriseus*. Chromosoma **79**, 179–198.

Feito, R.; Gallardo, M. (1982): Sperm morphology of the Chilean species of *Ctenomys* (Octodontidae). J. Mammalogy **63**, 658–661.

Hörz, W.; Zachau, H. G. (1977): Characterization of distinct segments in mouse satellite DNA by restriction nucleases. Eur. J. Biochem. **73**, 383–392.

Maniatis, R.; Fritsch, E. F.; Stambrook, J. (1982): Molecular cloning: a laboratory manual. Cold Spring Harbor, N.Y.: Cold Spring Harbor Laboratory.

Massarini, A. I.; Barros, M. A.; Ortells, M. O.; Reig, O. A. (1991): Chromosomal polymorphism and small karyotypic differentiation in a group of *Ctenomys* from central Argentina (Rodentia, Octodontidae). Genetica **83**, 131–144.

Ortells, M. O.; Contreras, J. R.; Reig, O. A. (1990): New *Ctenomys* karyotypes (Rodentia: Octodontidae) from north-eastern Argentina and from Paraguay confirm the extreme chromosomal multiformity of the genus. Genetica **82**, 189–201.

Reig, O. A. (1986): Diversity patterns and differentiation of high Andean rodents. In: High Altitude Tropical Biogeography. Ed. by F. Vuilleumier and M. Monasterio. New York, Oxford: Oxford University Press, Pp. 404–439.

Reig, O. A.; Busch, C.; Ortells, M. O.; Contreras, J. R. (1990): An overview of evolution systematics, population biology and speciation in *Ctenomys*. In: Evolutionary Biology of Subterranean Mammals. Ed. by E. Nevo and O. A. Reig. New York: Alan R. Liss. Pp. 71–96.

Reig, O. A.; Kiblisky, P. (1969): Chromosome multiformity in the genus *Ctenomys* (Rodentia: Octodontidae). A progress report. Chromosoma **28**, 211–244.

Rigby, P. W.; Dieckmann, M.; Rhodes, C.; Berg, P. (1977): Labeling desoxyribonucleic acid to high specific activity *in vitro* by nick translation with DNA polymerase I. J. Mol. Biol. **113**, 236–251.

Rossi, M. S.; Reig, O. A.; Zorzópulos, J. (1990): Evidence for rolling-circle replication in a major satellite DNA from the South American rodents of the genus *Ctenomys*. Mol. Biol. Evol. **7**, 340–350.

Southern, E. M. (1975): Detection of specific sequences among DNA fragments separated by gel electrophoresis. J. Mol. Biol. **98**, 503–517.

Vitullo, A. D.; Roldán, E. R. S.; Merani, M. S. (1988): On the morphology of spermatozoa of tuco-tucos, *Ctenomys* (Rodentia: Ctenomyidae): New data and its implications for the evolution of the genus. J. Zool. London **215**, 675–683.

Vitullo, A. D.; Cook, J. A. (1991): The role of sperm morphology in the evolution of tuco-tucos, *Ctenomys* (Rodentia, Ctenomyidae): Confirmation of results from Bolivian species. Z. Säugetierkunde **56**, 359–364.

Walsh, J. B. (1987): Persistence of tandem arrays: implications for satellite and simple-sequence DNA. Genetics **115**, 553–567.

Widegren, B.; Arnason, U.; Aküsjarvi, G. (1985): Characteristics of a conserved 1579-bp highly repetitive component in the killer whale *Orcinus orca*. Mol. Biol. Evol. **2**, 411–419.

Authors' addresses: María Susana Rossi, present address: Instituto de Investigaciones en Biología Molecular y Biotecnología (INGEBI), Vuelta de Obligado 2490-2do. Piso, RA-1428 Buenos Aires, Argentina; Jorge Zorzópulos, Departamento de Química Biológica, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Pabellón 2–4to. Piso, Ciudad Universitaria, RA-1428 Buenos Aires, Argentina

Z. Säugetierkunde 58 (1993) 252–255

ISSN 0044-3468

WISSENSCHAFTLICHE KURZMITTEILUNG

Disruption of territorial behaviour in badgers *Meles meles*

By T. J. Roper and P. Lüps

School of Biological Sciences, University of Sussex, United Kingdom and Naturhistorisches Museum der Burgergemeinde, Bern, Schweiz

Receipt of Ms. 13. 10. 1992
Acceptance of Ms. 29. 3. 1993

Badgers *(Meles meles)* typically live in mixed-sex social groups which defend permanent, communal and mutually exclusive territories (e.g. Kruuk 1978, 1989; Roper et al. 1986). Here we describe an unusual case in which a well-established and stable territorial system, involving several groups of badgers, was disrupted following the traumatic deaths of all the male members of one of the constituent social groups. The study was part of a longer-term investigation of badger behaviour and ecology in the South Downs, East Sussex, U.K. (for details of the study area and methods see Roper et al. 1986; Shepherdson 1986).

The data were collected between April 1986 and April 1988, and concern five neighbouring groups of badgers. From April to June 1986, group 1 consisted of five adult males, two females and one cub, of which four males were radio-collared and had been intensively radio-tracked. During the period June 21 to July 1 1986, all five males and the cub died, probably as a result of poisoning although post-mortem examination failed to confirm this. Following this incident, the two remaining females from group 1 (termed 1.1 and 1.2) were radio-collared on July 7, together with one male from each of groups 2 and 3 (2.1 and 3.1 respectively) and one male and two females from group 4 (4.1, 4.2 and 4.3 respectively). These animals were observed until October 1986, for at least 25 h per animal per month. In addition, bait-marking (Kruuk 1978) was carried out in April each year from 1984 to 1988, and in October 1986, on all 5 social groups. Badgers mark their territory boundaries by defecating at latrines (Roper et al. 1986), and the purpose of bait-marking was to allow territory boundaries to be mapped by determining which latrines were used by the members of each social group.

Bait-marking of setts 1–5, prior to the deaths of the group 1 males, showed the pattern typical of established territories in areas of high badger population density. Each main sett was surrounded by a network of latrines, such that the latrine systems of different setts defined contiguous and almost non-overlapping territories (Fig. 1a). By October 1986, however, three months after the death of the group 1 males, substantial overlap had appeared between territories 1 and 2 (Fig. 1b). At the same time, the whole of the area to the north-east of sett 1 was apparently no longer defended. By April 1987 (Fig. 1c), territories 1, 2 and 3 all overlapped considerably, to such an extent that territories 2 and 3 both encompassed the group 1 sett. A year later, however, in April 1988, the territorial situation had reverted to the original pattern, with territories 1–3 showing little overlap and their boundaries being more or less where they had been prior to the deaths of the group 1 males. The territories of groups 4 and 5 did not change subsequent to the deaths of the group 1 males, despite the fact that these territories were contiguous with that of group 1 and included latrines previously visited by members of group 1 (see Fig. 1a).

During the 2 years prior to the deaths of the males, members of group 1 never ventured more than 250 m into an adjacent territory and spent, on average, only 4.9 % of active time

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5804-0252 $ 02.50/0

outside their own territory. This is typical for our study area, where population density of badgers is high (about 12 adults/km^2) and territories are small (SHEPHERDSON 1986). Following the deaths of the group 1 males, however, the two remaining females almost immediately began to travel far into, and sometimes beyond, adjacent territories (Fig. 2a). Female 1.1 was first seen entering territory 5 on July 9th 1986, when she spent over an hour feeding there. During the following months she repeatedly travelled into or beyond territory 5, often feeding up to 1 km away from her original territory. In September and October she began regularly to enter territory 2, though occasional visits to territory 5 continued. Female 1.2 regularly ranged over large parts of territory 2 during the whole of the period July–October 1986, though she too occasionally visited territory 5. Both females repeatedly visited

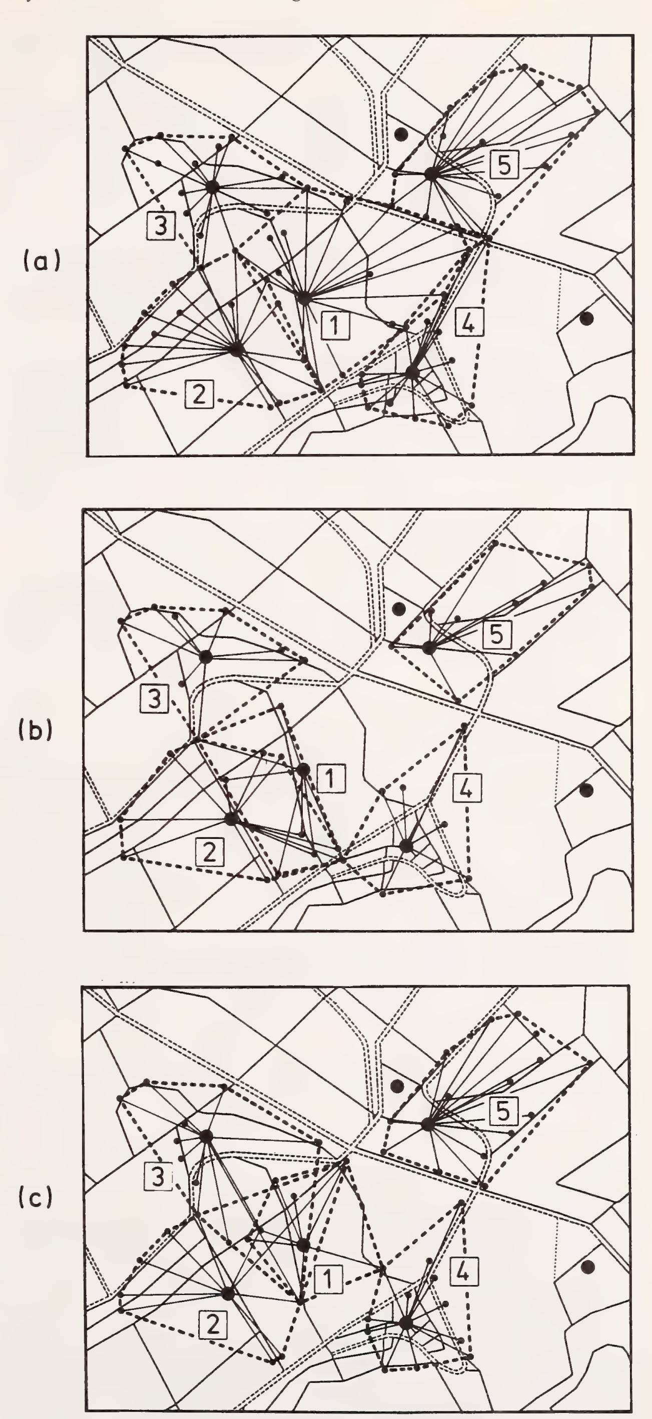


Fig. 1. Bait-marking maps showing territory boundaries (bold dashed lines) in (a) April 1984–1986 (data combined over all three years), (b) October 1986 and (c) April 1987. Territories are numbered 1 to 5. Large dots denote main setts, small dots denote latrines where bait-markers were found. Radial lines connect latrines where bait-markers were found to the main sett where the markers in question originated

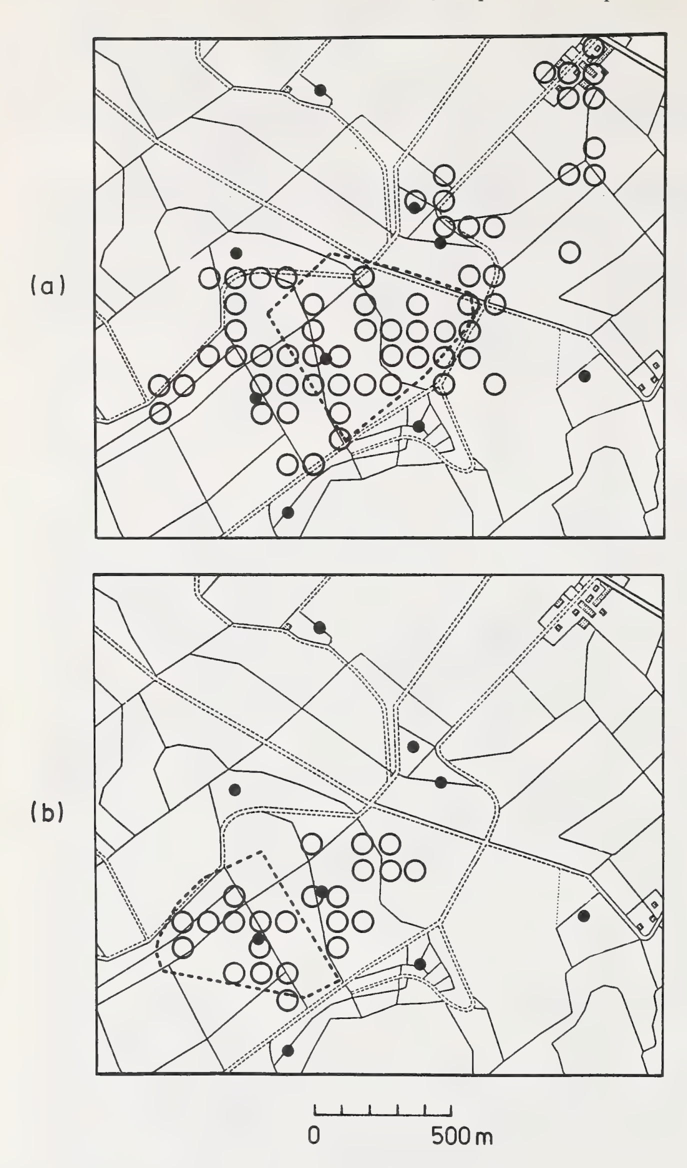


Fig. 2. Home ranges of (a) females 1.1 and 1.2 (data combined for both animals) and (b) male 2.1, during July–October 1986. The study area was divided into 0.25-ha grid squares (not shown), and open circles denote squares where the animals in question foraged. Filled circles show main setts; bold dashed lines show the original territory boundary, as determined by bait-marking, of (a) group 1 and (b) group 2

setts 2 and 5 and both were often seen feeding close to uncollared animals presumed to be members of groups 2 and 5: but no hostile interactions were observed.

From July 11 onwards, uncollared animals from neighbouring groups were repeatedly seen at sett 1 and elsewhere in territory 1, often in the company of one or other of the group 1 females. Male 2.1 ranged widely over territory 1 and regularly visited sett 1 (Fig. 2b). He also, on several occasions, foraged close to the group 1 females, either in his own territory or in theirs. Males 3.1 and 4.1, which were observed during the period July–October, also entered territory 1 on many occasions. Altogether, following the death of the group 1 males, females 1.1 and 1.2 spent 32 % and 25 % of their active time respectively outside the boundaries of their original territory, while for males 2.1, 3.1 and 4.1 the corresponding figures were 32 %, 28 % and 22 % respectively.

It is generally assumed that the primary purpose of territory defence in badgers is to monopolise food resources and that defence costs are shared by all members of a social group (see reviews by Kruuk 1989; Woodroffe and Macdonald 1993). However, it has also been suggested that territory defence is primarily a male activity and that its primary function is to deter neighbouring males from entering the territory for mating purposes (Roper et al. 1986). The dramatic changes in territorial and ranging behaviour that we

observed are, we believe, more readily explained by the mate-defence than by the food-defence hypothesis.

First, the group 1 territory rapidly decreased in size after the deaths of the resident males, and attempts to take it over were made by neighbouring groups, despite the fact that it was still inhabited by two females. Furthermore, the only neighbouring animals seen frequently to enter what was left of the group 1 territory were males. These observations suggest that males are more active than females both in territory defence and territory acquisition, and that resident males are the major deterrent to takeovers by adjacent groups (see also Kruuk 1978, 1989). Second, bait-marking showed that neighbouring groups only attempted to overlap parts of the original group 1 territory that were still being marked by the two females: no attempt was made to take over a large part of the group 1 territory that had apparently been vacated. This suggests that when neighbouring groups tried to expand their territories they were attempting to incorporate areas containing unguarded females, not to incorporate unused foraging areas. Third, the two group 1 females were repeatedly seen foraging in neighbouring territories, close to inhabitants of those territories, yet no aggressive interactions were seen. This suggests that territory holders are not primarily intent on monopolising food resources.

Acknowledgements

P. Lüps thanks the Burgergemeinde Bern for allowing him sabbatical leave at Sussex University; T. J. Roper thanks the SERC for financial support and Robinson Farms Ltd for permission to work on their land.

References

Kruuk, H. (1978): Spatial organisation and territorial behaviour of the European badger *Meles meles.* J. Zool. (London) **184,** 1–19.

Kruuk, H. (1989): The social badger. Oxford: Oxford University Press.

Roper, T. J.; Shepherdson, D. J.; Davies, J. M. (1986): Scent marking with faeces and anal secretion in the European badger. Behaviour **97,** 94–117.

Shepherdson, D. J. (1986): Foraging behaviour and space use in the European badger (*Meles meles* L.). DPhil. diss., Univ. Sussex.

Woodroffe, R.; Macdonald, D. W. (1993): Badger sociality – models of spatial grouping. Symp. Zool. Soc. Lond. **65,** 145–169.

Authors' addresses: Dr. T. J. Roper, School of Biological Sciences, University of Sussex, Brighton BN1 9QG, UK; Dr. P. Lüps, Naturhistorisches Museum, Bernastrasse 15, CH-3005 Bern, Switzerland

NICKEL, R.; SCHUMMER, A.; SEIFERLE, E.: **Lehrbuch der Anatomie der Haustiere.** Bd. I.: Bewegungsapparat. 6. völlig neubearbeitete Aufl. Berlin, Hamburg: Paul Parey 1992. 664 S., 607 Abb., DM 168,–. ISBN 3-489-58016-8

Fast 40 Jahre nach der ersten liegt nun eine völlig neubearbeitete 6. Auflage des 1. Bandes dieses Standardwerkes der Veterinäranatomie vor. Für diese Modernisierung sind J. FREWEIN (Zürich), K.-H. WILLE (Gießen) und H. WILKENS (Hannover), lehrerfahrene Anatomen mit unbestreitbarer Fachkompetenz tätig geworden. Sie haben aus Überzeugung den Charakter des Lehrbuches und die Anordnung der stofflichen Darbietung vorheriger Auflagen beibehalten, jedoch die Textabfassungen verständlicher gestaltet und gestrafft, Ergebnisse neuerer Studien eingearbeitet und die Nomina Anatomica Veterinaria konsequent angewandt. Auch einige Abbildungen wurden durch neue ersetzt, der Gesamtumfang des Bandes blieb jedoch weitgehend erhalten.

In der Einleitung dieses Bandes wird in Kürze eingegangen auf systematische Stellung der Haussäugetiere, Einteilung des Körpers in Organe und Organsysteme, Lagebeziehungen am Körper und Einteilung in Körpergegenden. Im Hauptteil wird der Bewegungsapparat eingehend beschrieben als Skelettsystem (mit Knochenlehre und Gelenklehre) in seinem passiven und als Muskelsystem im aktiven Anteil. Die Beschreibungen erfolgen, der Körpergliederung entsprechend, jeweils zunächst in einer allgemeinen Darstellung der Situation, anschließend werden Besonderheiten bei Fleischfressern (Hund, Katze), Schwein, Wiederkäuern (Rind, Schaf, Ziege) und Pferd (Esel) aus vergleichender Sicht geboten. Die funktionelle Bedeutung im komplexen Gefüge der verschiedenen Elemente wird stets hervorgehoben, vor allem bei der Besprechung der Muskulatur. Hier wird im Anschluß an die allgemeinen Beschreibungen der Körperregionen die Innervation von individuellen Muskeln und Muskelgruppen durch Hauptnerven und deren Rami tabellarisch gelistet.

Insgesamt liegt eine in Wort und Bild beeindruckende neue Auflage mit ansprechender Ausstattung vor. Für Studenten der Veterinärmedizin und praktizierende Tierärzte ist sie von besonderem Wert, aber auch Säugetierkundler mit spezieller Fragestellung werden diesen Band mit Gewinn nutzen.

D. KRUSKA, Kiel

CORBET, G. B.; HILL, J. E.: **The Mammals of the Indomalayan Region.** A Systematic Review. Oxford, Toronto, New York: Oxford University Press 1992. 488 pp., 45 figs., 273 tabs., 177 maps. £ 60.00. ISBN 0-19-854693-9

The mammalian fauna of the major zoogeographical regions of the world has been documented more or less precisely except for the Indomalayan or Oriental Region. Only certain parts of this region have been dealt with in previous publications. Scattered information on circumscribed areas, such as islands, has remained more or less unknown to the western scientific community. Therefore, the authors of this book attempt to summarize what is known about the mammalian species of this part of the world, especially concerning their taxonomic status and distribution. Both authors are very much aware of uncertainties in many cases. Nevertheless, they have made a concerted effort to review the literature critically also using the collections of the Natural Museum of History in London as well as those of many other institutions for this purpose.

An introductory chapter is devoted to some generally valid information on, e. .g., boundaries of the total Indomalayan region and of six subregions and several divisions; a time-scale; short history of the scientific discoveries and survey of recent literature; classification; nomenclature; identification; distribution, ecology, conservation, and some other topics. The diverse species of this region are then treated in the main section of the book. Species of two marsupial (Peramelina, Diprotodontia) and 15 eutherian orders (Pholidota, Insectivora, Scandentia, Dermoptera, Chiroptera, Primates, Carnivora, Cetacea, Proboscidea, Sirenia, Perissodactyla, Tubulidentata, Artiodactyla, Rodentia, Lagomorpha) are listed and their prominent morphological and anatomical features are described in addition to distribution range, ecology, and variation. In some cases special remarks are added. Extinct as well as extant species are listed, and also domesticated forms are included. Here, a certain inconsequence must, however, be mentioned concerning the taxonomic status of these mammalian forms. It is generally accepted that certain wild species and their domesticated derivatives are still of the same species since domestication has not led to the creation of new species. It therefore seems incorrect to classify both forms into two differently named species. This special problem of taxonomy was unfortunately not taken into account here although it had been solved earlier.

Nevertheless, besides these and other uncertainties, this is an imposing treatise that offers a wealth of information including many unresolved questions. It can be recommended as a basic guideline, upon which future improvements can be made.

D. KRUSKA, Kiel



Erscheinungsweise und Bezugspreis 1993: 6 Hefte bilden einen Band. Jahresabonnement Inland: DM 378,– zuzüglich DM 13,80 Versandkosten; Jahresabonnement Österreich: öS 2940,– zuzüglich öS 140,– Versandkosten; Jahresabonnement Schweiz: sfr 364,– zuzüglich sfr 17,50 Versandkosten; Jahresabonnement EG-Binnenmarkt-Länder mit USt-ID-Nr.: DM 354,– zuzüglich DM 16,82 Versandkosten; Jahresabonnement EG-Binnenmarkt-Länder ohne USt-ID-Nr. und Drittländer: DM 378,– zuzüglich DM 18,– Versandkosten. Das Abonnement wird zum Jahresanfang berechnet und zur Zahlung fällig. Es verlängert sich stillschweigend, wenn nicht spätestens am 15. November eine Abbestellung im Verlag vorliegt. Die Zeitschrift kann bei jeder Buchhandlung oder bei der Verlagsbuchhandlung Paul Parey GmbH & Co. KG, Spitalerstraße 12, W-20095 Hamburg, Bundesrepublik Deutschland, bestellt werden. Die Mitglieder der „Deutschen Gesellschaft für Säugetierkunde" erhalten die Zeitschrift unberechnet im Rahmen des Mitgliedsbeitrages.

Vol. 58 (5), 257–320, Oktober 1993 ISSN 0044-3468 C 21274 F

ZEITSCHRIFT FÜR SÄUGETIERKUNDE

INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Organ der Deutschen Gesellschaft für Säugetierkunde



Verlag Paul Parey Hamburg und Berlin

This journal is covered by Biosciences Information Service of Biological Abstracts, and by Current Contents (Series Agriculture, Biology, and Environmental Sciences) of Institute for Scientific Information

Die Zeitschrift für Säugetierkunde veröffentlicht Originalarbeiten und wissenschaftliche Kurzmitteilungen aus dem Gesamtgebiet der Säugetierkunde, Besprechungen der wichtigsten internationalen Literatur sowie die Bekanntmachungen der Deutschen Gesellschaft für Säugetierkunde. Verantwortlicher Schriftleiter im Sinne des Hamburgischen Pressegesetzes ist Prof. Dr. Dieter Kruska.

Zusätzlich erscheint einmal im Jahr ein Heft mit den Abstracts der Vorträge, die auf der jeweiligen Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde gehalten werden. Sie werden als Supplement dem betreffenden Jahrgang der Zeitschrift zugeordnet. Verantwortlich für ihren Inhalt sind ausschließlich die Autoren der Abstracts.

Manuskripte: Manuskriptsendungen sind zu richten an die Schriftleitung, z. Hd. Prof. Dr. Dieter Kruska, Institut für Haustierkunde, Biologiezentrum der Christian-Albrechts-Universität, Am Botanischen Garten 9, D-24118 Kiel, Bundesrepublik Deutschland. Für die Publikation vorgesehene Manuskripte sollen gemäß den „Redaktionellen Richtlinien" abgefaßt werden. In ihnen finden sich weitere Hinweise zur Annahme von Manuskripten, Bedingungen für die Veröffentlichung und die Drucklegung, ferner Richtlinien für die Abfassung eines Abstracts und eine Korrekturzeichentabelle. Die Richtlinien sind auf Anfrage bei der Schriftleitung und dem Verlag erhältlich.

Sonderdrucke: Anstelle einer Unkostenvergütung erhalten die Verfasser von Originalbeiträgen und Wissenschaftlichen Kurzmitteilungen 50 unberechnete Sonderdrucke. Mehrbedarf steht gegen Berechnung zur Verfügung, jedoch muß die Bestellung spätestens mit der Rücksendung der Korrekturfahnen erfolgen.

Fortsetzung 3. Umschlagseite

 Verlag: Paul Parey GmbH & Co. KG, Hamburg und Berlin. Anschriften: Spitalerstr. 12, D-20095 Hamburg; Seelbuschring 9–17, D-12105 Berlin, Bundesrepublik Deutschland. – Printed in Germany by Westholsteinische Verlagsdruckerei Boyens & Co., Heide/Holst.

Z. Säugetierkunde 58 (1993) 257–265

ISSN 0044-3468

Olfaktorische Kommunikation bei der Kleinen Lanzennase, *Phyllostomus discolor* (Chiroptera, Phyllostomidae)

Von P. Höller und U. Schmidt

Zoologisches Institut der Universität Bonn, Deutschland

Eingang des Ms. 3. 8. 1992
Annahme des Ms. 26. 2. 1993

Abstract

Olfactory communication in the Lesser spear-nosed bat, Phyllostomus discolor (Chiroptera, Phyllostomidae)

Male *Phyllostomus discolor* are able to distinguish between the own and another male's marking odour. When their preferred roosting-site was marked by a strange male, they increased the amount of time spent there, but, however, not at an alternative site, when the same mark was present. The amount of time at the preferred site did not increase in response to the presence of own odour, while own odour at an alternative site resulted in increased time spent there.

Female *P. d.* reacted to a non-harem-male's odour at their roosting-site with an increase in motor activity but not an increase in the time spent there. The odour of the familiar harem male evoked little behavioural response.

Einleitung

Die neotropische Fledermaus *Phyllostomus discolor* (Kleine Lanzennase, Phyllostomidae) lebt in sozialen Verbänden, die bis zu vierhundert Individuen umfassen können (Bradbury 1977). Diese Großgruppen finden ihr Tagesquartier zumeist in hohlen Bäumen, wo sie stabile soziale Substrukturen etablieren, die in drei Klassen eingeteilt werden können: 1. Harems (one male groups), Kleingruppen mit einem ♂ und bis zu 15 ♀♀ (Wilkinson 1987); 2. Junggesellengruppen (bachelor groups): Kleingruppen, die ausschließlich aus subadulten, bzw. nicht haremsbildenden adulten ♂♂ bestehen; 3. einzeln lebende Tiere beiderlei Geschlechtes (Beobachtung im Labor).

Zur Etablierung und Aufrechterhaltung dieser Substrukturen muß aufgrund der ungünstigen Orientierungs- und Kommunikationsbedingungen innerhalb der Quartiere eine räumliche Konstanz der Kleingruppen gegeben sein. Gruppengebundene ♂♂ – insbesondere Haremsmännchen – erweisen sich als extrem ortstreu (in der Versuchskolonie unseres Labors blieben die Harems über zwei Jahre am gleichen Platz). Die Haremsmännchen suchen diesen Platz nach der Futtersuche immer wieder auf und verteidigen ihn gegen eindringende ♂♂. Weibliche Tiere scheinen dagegen weniger ortsgebunden zu sein. Sie können über längere Zeit an eine spezifische Gruppe gebunden bleiben, einige ♀♀ wechseln aber auch häufiger den Harem (Fenton und Kunz 1977; eigene Beobachtung im Labor).

Neben taktiler und akustischer Kommunikation scheint die Olfaktorik im Gruppenleben der Kleinen Lanzennase eine bedeutsame Rolle zu spielen. Dominante ♂♂ zeigen ein häufig auftretendes Markierungsverhalten: sie streichen mit charakteristischen Bewegungen die Hals-Brustregion, die sich bei männlichen *P. discolor* durch die gut sichtbare Ausführöffnung einer Hautdrüse (Valdivieso und Tamsitt 1964) auszeichnet, über das Substrat und die Mitglieder der eigenen Gruppe.

Während für Fledermäuse die olfaktorische Kommunikation zwischen Jungtieren und ihren Müttern experimentell gut belegt ist (Kolb 1977; Gustin und McCracken 1987), sind Experimentaldaten über ein Markierungsverhalten innerhalb eines „inneren Territo-

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5805-0257 $ 02.50/0

riums" rar (Buchler 1980; Häussler und Nagel 1984). Da nicht nur bei der sozialen Kontaktaufnahme, sondern auch beim Aufsuchen des eigenen Hangplatzes intensives Riechen am Substrat, bzw. dem Sozialpartner stattfindet, ist zu vermuten, daß olfaktorische Marken sowohl im sozialen Kontext, als auch bei der Orientierung von Bedeutung sind.

Diese Untersuchung befaßt sich mit der Fähigkeit von *P. discolor,* differenziert auf Markierungsdüfte von Artgenossen zu reagieren, und sie erbringt Hinweise dafür, daß die olfaktorische Kommunikation im komplexen Sozialverhalten der Kleinen Lanzennase eine wichtige Rolle spielt.

Material und Methoden

Die Untersuchungen wurden an vier adulten Individuen (2 ♂♂, 2 ♀♀) der Kleinen Lanzennase durchgeführt. Alle untersuchten Tiere kamen aus der gleichen, im Zoologischen Institut der Universität Bonn gehaltenen Kolonie, deren Individuenbestand während der Versuchszeit mit 20 Tieren stabil blieb. Die Fledermäuse leben in einem künstlichen Tag-Nacht-Rhythmus (LD 12:12); relative Luftfeuchtigkeit (ca. 80 %) und Temperatur (ca. 25°) werden konstant gehalten. Um die Individuen unterscheiden zu können, wurden ihnen auf dem Rücken die Haare in verschiedenen Mustern auf etwa einen Millimeter zurückgeschnitten. Da die Tiere ein weißes Unterfell besitzen, sind die Markierungen auch bei schwacher Beleuchtung gut zu erkennen.

Die räumliche Verteilung der Individuen wurde innerhalb der Kolonie sowohl während der Hellphase als auch während der Dunkelphase (Nachtsichtgeräte Noctron IV, Euroatlas GmbH und Metascope, VARO Inc.) beobachtet. Die Experimente wurden in einem 300 × 80 × 80 cm großen Flugtunnel durchgeführt (Abb. 1a). Dieser allseits aus glattem Hartplastik (Trovidur™) aufgebaute Tunnel war dreigeteilt, so daß die Tiere einen Aufenthaltsraum besaßen, der durch eine Schiebetür gegen den Flugraum verschließbar war. Die sich anschließende Flugarena war 250 cm lang, wobei die Fledermäuse, um die gegenüberliegende Stirnwand zu erreichen, eine Blende unterfliegen mußten, die kurz vor der Stirnwand eingehängt war. Als Landefläche war ein 40 × 20 cm großes Trovidur™-Gitter 10 cm über dem Boden der Anlage in die Stirnwand eingelassen. Als Ruhegitter waren rechts und links des Landegitters 15 × 25 cm große Rahmen in die Zielwand eingehängt, deren obere Hälfte mit Trovidur™-Gitter, die untere mit undurchbrochenem Plastik beklebt war. Diese beiden Ruheplätze waren für die Tiere nur durch vertikales Laufen auf dem Landegitter zu erreichen, da sie durch das Unterfliegen der Blende den unteren Rand der Hangplätze nicht erreichen konnten.

Bei den Experimenten handelte es sich um Zweifach-Präferenzwahlen ohne Konditionierung durch Belohnung. In den kritischen Versuchen wurde eines der beiden Ruhegitter in einem kleinen Käfig von männlichen Tieren aus der Kolonie beduftet. Die Duftdonatoren wurden dazu eine Stunde in diesem Käfig gehalten. Anschließend wurde das Versuchstier in den Aufenthaltsraum gesetzt und die Stirnwand der Anlage mit zwei Ruhegittern und dem Landegitter ausgestattet. Mit den vier Tieren wurden jeden Tag fünf einzelne Versuche durchgeführt, die je eine Zeitbegrenzung von zehn Minuten hatten und immer mit einem Blindversuch, bei dem zwei unbeduftete Ruheplätze eingehängt waren, begonnen wurden.

Mit den beiden ♂♂ und einem ♀ wurden zwei Versuchsansätze durchgeführt, die sich durch die Duftdonatoren unterschieden (das zweite ♀ absolvierte nur einen Versuch). Die Versuchsbezeichnung „α-0" beschreibt Untersuchungen, in denen als Duftdonator ein stark dominantes ♂ aus der Kolonie eingesetzt wurde. Die Bezeichnung „e-0" (nur bei ♂♂) bedeutet, daß das Versuchstier das Gitter selbst beduftet hatte. Mit einem ♀ wurde der Versuch „h-0" durchgeführt, hier wurde ein Hangplatzgitter vom Harems-♂ des Versuchstieres beduftet.

Mit Hilfe eines Epson Laptop Computer PX8 wurden die folgenden Daten gesammelt, bzw. errechnet.

1. Dauer der einzelnen Aufenthalte der Tiere auf den Ruhegittern,
2. Gesamtaufenthaltsdauer (die Zeit, die ein Tier während eines Versuchsdurchlaufs auf jeweils einem der Ruhegitter verbracht hat),
3. mittlere Aufenthaltsdauer,
4. Aufenthaltshäufigkeit der Tiere auf je einem der Ruhegitter,
5. Anflughäufigkeit auf das Landegitter.

Ergebnisse

Blindversuche

Bei den täglich durchgeführten Blindversuchen, bei denen beide Ruhegitter duftlos waren, zeigte sich eine deutliche Seitenstetigkeit aller Versuchstiere. ♂♂ und ♀♀ bevorzugten den

linken Ruheplatz, so daß eine Betrachtung der Gesamtaufenthaltszeiten auf den Ruhegittern eine links-rechts-Verteilung von 90 % : 10 % ergibt. Das Ausmaß der Seitenstetigkeit (Hangplatztreue) ist geschlechtsabhängig. Obwohl ♂♂ und ♀♀ insgesamt etwa gleichlang an der Zielwand verweilten (♀: 142s; ♂: 156s), zeigte sich, daß die Seitenstetigkeit bei den ♀♀ stärker ausgeprägt ist, als bei den ♂♂. Während die ♀♀ im Durchschnitt 99 % der Zeit auf dem Präferenzplatz zu finden waren, bevorzugten die ♂♂ den Präferenzplatz mit nur 82 % (Abb. 1b). In vielen Versuchen wurde das rechte Gitter von den ♀♀ ganz gemieden, während sich die ♂♂ in jedem Versuch zumindest für kurze Zeit dort aufhielten. Die Bevorzugung des linken Hangplatzes wurde auch in Versuchen mit olfaktorischen Marken auf den Ruhegittern nicht aufgegeben.

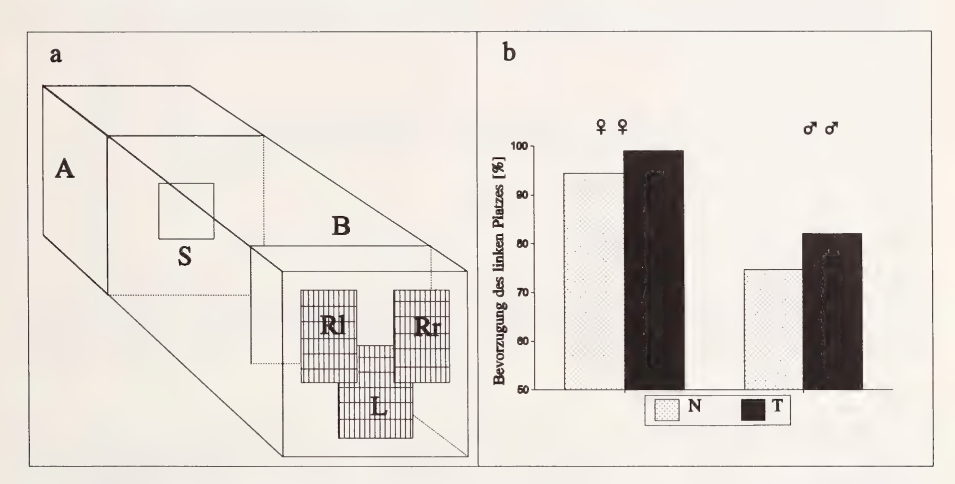


Abb. 1. a: Skizze der Versuchsarena. A Aufenthaltsraum, B zu unterfliegende Blende, L Landegitter, Rl(Rr) linkes (rechtes) Ruhegitter, S Startklappe; b: Bevorzugung des linken Hangplatzes durch ♀♀ bzw. ♂♂ in den Blindversuchen. Dargestellt sind die %-Anteile der Anflughäufigkeit (N), bzw. der Aufenthaltsdauer (T) am linken Gitter

Da die Bevorzugung des linken Platzes quantitativ von Tag zu Tag schwanken konnte, scheint es wenig sinnvoll, die Daten der kritischen Experimente mit dem Mittelwert, bzw. Median aller Blindwerte zu vergleichen. Daher wird das Maß der Präferenz folgendermaßen berechnet.

Für jeden Versuchsdurchgang wird ermittelt, wie häufig und wie lange sich ein Tier an jedem der beiden Plätze aufhielt. Die Anflughäufigkeit und die Verweildauer auf dem rechten bzw. dem linken Gitter werden prozentual zur Gesamtzahl aller Anflüge bzw. der Gesamtzeit auf beiden Gittern angegeben. Zur Darstellung der effektiven Verhaltensrelevanz der olfaktorischen Marken werden die prozentualen Verteilungen der kritischen Experimente mit den Prozentdaten der Blindversuche des gleichen Tages verglichen und als Differenz dargestellt. Diese täglich ermittelten Differenzen werden zur Darstellung (Abb. 2, 3) über den gesamten Versuchszeitraum gemittelt.

Der tägliche Vergleich der kritischen Experimente mit den Ergebnissen der Blindversuche verhindert eine zu starke Einflußnahme der von Tag zu Tag unterschiedlich ausgeprägten Neigung zu explorieren.

Experiment „e-0“: Eigenduft vs. Leer (♂♂)

Die von den männlichen Versuchstieren selbst bedufteten Hangplatz-Gitter wurden nach einem einführenden Blindversuch in pseudozufälliger Reihenfolge rechts (i. F. „RM-

Versuch") oder links („LM-Versuch") an der Zielwand der Versuchsanlage montiert, der jeweils andere Ruheplatz blieb unbeduftet.

Beide ♂♂ reagierten mit einem veränderten Hangplatzverhalten, wenn das markierte Gitter auf der rechten Seite, also dem nicht präferierten Hangplatz, montiert war (Abb. 2, unten). Sowohl bezüglich der Aufenthaltszeit, als auch der Häufigkeit, mit der die Plätze jeweils aufgesucht wurden, nahm die Bevorzugung der linken, zugunsten der rechten Seite ab. In „LM"-Versuchen war dagegen bei beiden ♂♂ keine signifikante Verhaltensänderung feststellbar (Abb. 2, oben). Dies zeigt, daß die Tiere auf die unterschiedlichen Situationen (eigene Marke am fremden Platz bzw. am Präferenzplatz) differenziert reagieren: Der Eigenduft auf dem Hangplatz, der normalerweise nur sehr selten aufgesucht wird, führt dort zu einer deutlich erhöhten Präsenz; ist der eigene Markierungsgeruch jedoch auf dem präferierten Ruheplatz wahrnehmbar, so hat dies keinen Effekt auf das Hangplatzverhalten.

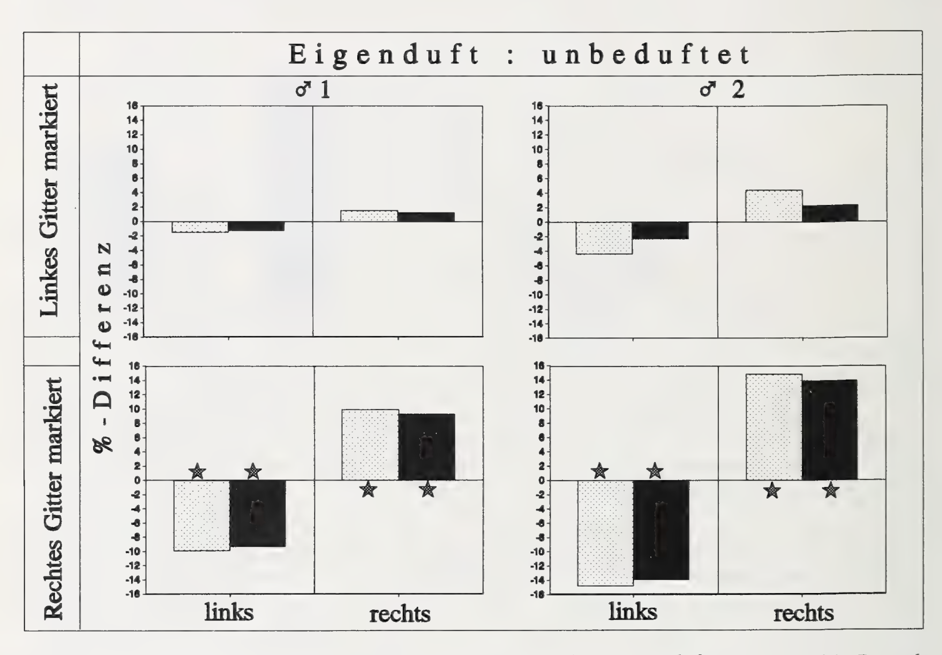


Abb. 2. Verschiebung der Hangplatzpräferenz in den Versuchen „Eigenduft vs. Leer" (♂♂) Darstellung der prozentualen Abweichung der Anflughäufigkeit (helle Säulen) bzw. der Gesamtaufenthaltsdauer (dunkle Säulen) vom jeweiligen Blindwert (Nullinie). * Signifikanter Unterschied zum Blindwert (Mann-Whitney-U-Test, $p < 0{,}05$)

Experiment „α-0": α-Duft vs. Leer (♂♂)

Ein Hangplatzgitter wurde vor den Versuchen von einem stark dominanten ♂ aus der Kolonie beduftet. Nach je einem einführenden Blindversuch wurde dieses Gitter in pseudozufälliger Reihenfolge auf eine Seite der Zielwand eingehängt.

War das olfaktorisch markierte Gitter auf dem rechten, also dem nicht präferierten Hangplatz angebracht, so reagierte keines der beiden ♂♂ quantifizierbar auf den α-Geruch (Abb. 3, unten). In Versuchen dagegen, in denen der Präferenzplatz durch das dominante ♂ markiert war, erhöhte ♂ 1 dort seine Präsenz signifikant (Abb. 3, oben). Während dieser Zeit kam es kaum zu ruhigen Phasen, in denen das Tier unbeweglich blieb, es lief

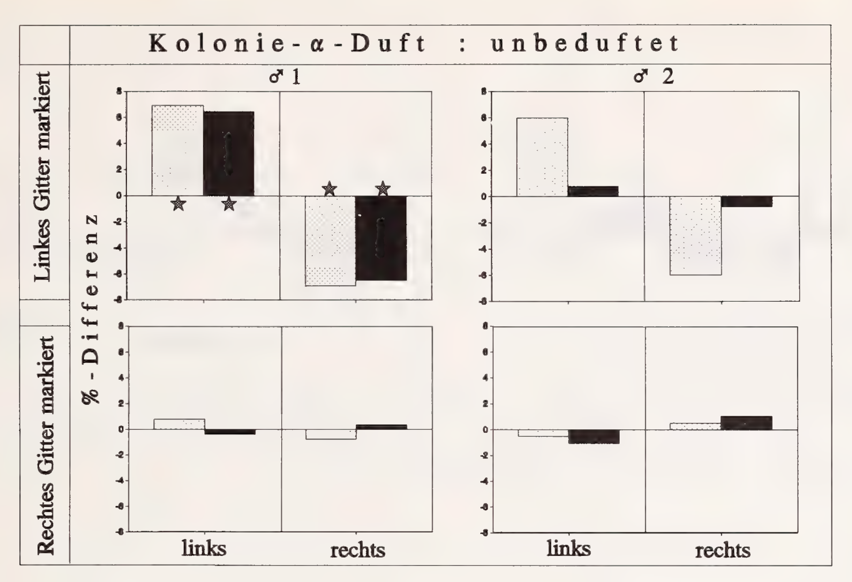


Abb. 3. Verschiebung der Hangplatzpräferenz in den Versuchen „α-Duft vs. Leer" (♂♂) Darstellung der prozentualen Abweichung der Anflughäufigkeit (helle Säulen) bzw. der Gesamtaufenthaltsdauer (dunkle Säulen) vom jeweiligen Blindwert (Nullinie).* Signifikanter Unterschied zum Blindwert (Mann-Whitney-U-Test, $p < 0{,}05$)

statt dessen während der ganzen Zeit unruhig auf dem Gitter herum (ein Verhalten, das in Blindversuchen nie derart ausgeprägt zu beobachten war).

Die Auswertung der Daten aus der gleichen Versuchsserie mit ♂ 2 (Abb. 3 oben, rechte Graphik) zeigte keine statistisch sicherbare Tendenzen bezüglich einer Präferenzverschiebung. Trotzdem war auch hier am Verhalten des Tieres eine Beeinflussung durch den Duft zu beobachten, so daß es lohnend erschien, die Versuchsdaten eingehender zu untersuchen, um nicht durch die Mittelung der Daten Ergebnisse zu verdecken.

In Abbildung 4 werden für ♂ 2 die Differenzwerte jedes einzelnen Versuches in einem ungemittelten Flächendiagramm dargestellt, so daß es möglich ist, längerfristige Verhaltensänderungen des Versuchstieres deutlich zu machen. In den „LM"-Versuchen erkennt man eine Periodizität der Verhaltensantwort. Phasen, in denen die Markierung auf dem Präferenzplatz dort eine höhere Präsenz des ♂ auslösen, wechseln mit Phasen ab, in denen der Präferenzplatz eher gemieden wird (Abb. 4a). Diese Periodizität läßt sich mit Hilfe der Sequenzanalyse (Siegel 1985) statistisch sichern. Sie läßt sich weder für die Ergebnisse der „e-0"-Serie noch für die α-0-RM-Versuche bestätigen (Abb. 4b), so daß es sich hier um einen speziellen Effekt der α-Markierung auf dem Präferenzplatz handelt.

Experiment „α-0": α-Duft vs. Leer (♀♀)

♀ 1 zeigte weder in „LM"-, noch in „RM"-Versuchen eine statistisch sicherbare Verhaltensantwort auf den Duft des Kolonie-α-♂. Es blieb in allen Versuchen zu ca. 99,3 % (LM-Versuche) bzw. 97,6 % (RM-Versuche) der Zeit auf dem linken Hangplatz.

Auch ♀ 2 war bei den Blindversuchen nahezu ausschließlich auf dem linken Hangplatz zu finden. Bei Beduftung sowohl dieses Präferenzplatzes, als auch des Alternativplatzes wechselte es signifikant häufiger („LM"-Versuche: 8,2 %; „RM"-Versuche: 7,6 %) und für längere Zeit („LM"-Versuche: 6,6 %; „RM"-Versuche: 2,53 %) die Seite als in Blindversuchen.

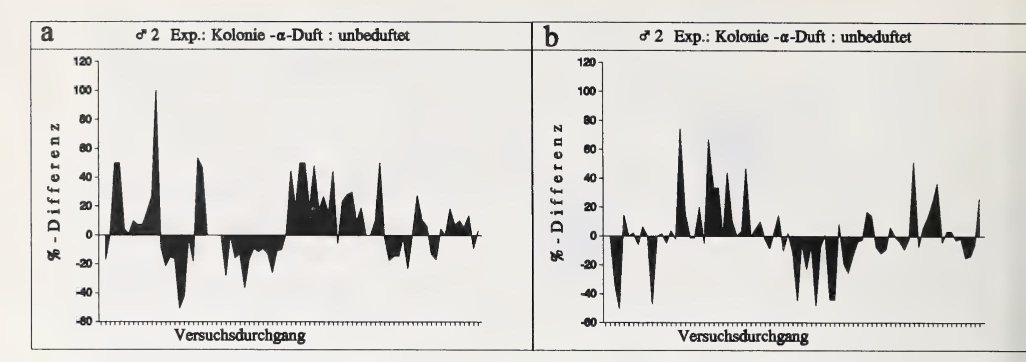


Abb. 4. Prozentuale Abweichung der Aufenthaltsdauer am α-Duft-markierten Gitter von den Blindwerten des gleichen Versuchstages (4a „LM"-Versuche; 4b „RM"-Versuche). Die prozentuale Differenz jedes einzelnen Versuchs zum Blindwert ist als Eckpunkt der Flächendiagramme eingetragen. Dargestellt sind nur die Daten des jeweils markierten Hangplatzes

Experiment „h-0": Duft des eigenen Harems-♂ vs. Leer (♀ 2)

Aus versuchstechnischen Gründen konnte diese Versuchsserie mit nur einem ♀ durchgeführt werden. Es ergaben sich keine statistisch sicherbaren Änderungen gegenüber dem Verhalten in Blindversuchen.

Diskussion

Die Fähigkeit zur innerartlichen Kommunikation ist eine der wesentlichen Voraussetzungen zur Bildung sozialer Gruppen im Tierreich. Akustische, visuelle, taktile und olfaktorische Kommunikationsformen können bei Interaktionen sozialer Tiere beobachtet werden. Gerade bei den Chiropteren, die zum Teil außerordentlich große soziale Gruppen bilden, ist die Frage nach den Kommunikationsformen interessant, da die Fledermäuse durch die Entwicklung des Fluges und der nachtaktiven Lebensweise viele Spezialisationen ausgebildet haben.

Bei den nachtaktiven und zum großen Teil in geschlossenen Quartieren lebenden Fledermäusen ist es unwahrscheinlich, daß die visuelle Kommunikation eine wichtige Rolle im sozialen Leben spielt, obwohl die visuellen Leistungen verschiedener Arten erstaunlich gut entwickelt sind (Bell 1986; Manske und Schmidt 1976; Suthers et al. 1969). Aufgrund der hervorragenden auditorischen Leistungen der Fledermäuse, sowie ihrer höchst differenzierten Vokalisierungsfähigkeit eignen sich akustische Signale besonders gut zur Kommunikation innerhalb der Fledermaus-Verbände. Ein breites Spektrum verschiedenartiger Soziallaute ist für viele Chiropteren beschrieben und deutet auf intensive akustische Interaktionen (August 1985; Esser und Schmidt 1989; Porter 1979). Über taktile Verständigungsformen ist in dieser Tiergruppe nur wenig bekannt.

Ausgedehnte exokrine Drüsenfelder in der Gesichtsregion vieler Fledermausarten z. B. in den Familien Vespertilionidae (Schmidt et al. 1989) oder Rhinopomatidae (Kulzer et al. 1985), bzw. unpaarige Drüsen mit einem zentralen Ausführgang in der Hals- und Brustregion einiger Emballonuridae (Pandey und Dominic 1987), Molossidae (Werner und Lay 1963) und den Arten der Gattung *Phyllostomus* (Valdivieso und Tamsitt 1964), weisen darüber hinaus auf olfaktorische Kommunikation hin. Wie in zurückliegenden Arbeiten gezeigt werden konnte, sind die olfaktorischen Leistungen aller untersuchten Fledermausarten ausreichend für eine olfaktorische Kommunikation (Laska und Schmidt 1986; Laska 1990; Schmidt und Schmidt 1978). Aufgrund verschiedener physikalischer

Gesetzmäßigkeiten der Ausbreitung olfaktorischer Signale eignen sich diese besonders zur sozialen Informationsübertragung:

- Eine Duftquelle ist von mehreren Rezipienten gleichzeitig und über eine begrenzte Entfernung wahrnehmbar.
- bei der Diffusion der Geruchsstoffe in den Luftraum bildet sich ein deutlicher Gradient, der eine Lokalisierung der Reizquelle zuläßt,
- chemische Markierungen (olfaktorisch und gustatorisch) sind die einzige Möglichkeit eines Tieres, Informationen über sein Alter und Geschlecht, seinen Sexual- und Sozialstatus, seine Gruppenzugehörigkeit und vieles andere bis hin zu Informationen über seine momentane emotionale Lage zu hinterlassen (Brown und MacDonalds 1985).

Während rein beschreibende Hinweise auf die Sozialrelevanz der Olfaktorik bei Fledermäusen für verschiedene Arten zu finden sind (Bradbury und Emmons 1974; Häussler 1989), bleiben experimentelle und quantifizierende Untersuchungen zu diesem Thema rar (Mutter-Jungtier-Erkennung: Kolb 1977; Gustin und McCracken 1987; Adult-Adult-Interaktionen: Gustin und McCracken 1987).

Aufgrund der Neigung von *Phyllostomus discolor,* auch isoliert in einer Versuchsanlage einen Präferenzplatz zu wählen und diesen mit erstaunlicher Ortskonstanz zu bevorzugen, erweist sich diese Spezies für experimentelle Ansätze zur Erforschung der Sozialrelevanz der Olfaktorik als besonders geeignet.

Die deutlichere Ausprägung der Ortskonstanz der ♀♀ in der Versuchsanlage scheint zunächst im Widerspruch zu den Beobachtungen in der Kolonie zu stehen, wo die männlichen Tiere angestammte Plätze über lange Zeit besetzt halten und verteidigen, während die ♀♀ häufiger Ortswechsel unternehmen. Dieser Widerspruch löst sich unter Berücksichtigung der fehlenden sozialen Kontakte in der Anlage auf. Die getesteten ♂♂ konnten ohne territorialen Konkurrenzdruck durch exploratives Verhalten verschiedene Plätze untersuchen. Für die in der Kolonie haremsgebundenen ♀♀ scheint es viel eher von Bedeutung zu sein, sich einer Gruppe anzuschließen, die am Stammplatz eines in der Ressourcenkonkurrenz erfolgreichen ♂ angesiedelt ist (für *Pipistrellus:* Gerell und Lundberg 1985). So erweist sich für die ♀♀ die olfaktorische Marke eines einzelnen ♂ als nicht relevant für die Bevorzugung eines Hangplatzes, obgleich im Verhalten sehr deutlich wurde, daß beide getesteten ♀♀ die Markierung wahrnehmen und eingehend olfaktorisch untersuchen.

Bei der Auswertung der gewählten Verhaltensparameter „Aufenthaltsdauer“ und „Anflughäufigkeit“ ist allerdings auffällig, daß ♀ 2 mit erheblich gesteigerter Unruhe (verkürzte mittlere Aufenthaltsdauer nach jedem Anflug) auf den α-Geruch reagierte, wogegen der Geruch des eigenen Haremsmännchens zu einer ruhigeren olfaktorischen Inspektion des Präferenzplatzes führte, so daß man davon ausgehen kann, daß dieses Tier in der Lage ist, individuelle Unterschiede in den Markierungen festzustellen.

In den kritischen Experimenten mit männlichen *P. discolor* wurden zunächst Duftmarken des Kolonie-α-♂ auf den Hangplätzen angeboten. Nach dem *pars pro toto* – Modell des Individualgeruches (BILZ 1940) haben derartige Marken eine Stellvertreterfunktion, die die Anwesenheit des Donators symbolisiert. Bei sozial lebenden und territorialen Arten sind bei ♂♂ Reaktionen auf derartige „Stellvertreter“ unter verschiedenen Motivationszuständen des Versuchstieres denkbar. Es kann ebenso territoriales Verhalten ausgelöst werden, wie auch eine Bereitschaft zu sozialer Kontaktaufnahme. Im Versuch war es möglich, diese unterschiedlichen Motivationen zu trennen.

War der Geruch des Duftdonators am Präferenzplatz wahrnehmbar, so erhöhte ♂ 1 dort deutlich seine Präsenz, während das Verhalten von ♂ 2 wechselte. Phasenweise erhöhte es seine Präsenz am bevorzugten Hangplatz, zeitweise wich es der olfaktorischen Markierung aus. Auf die gleiche Duftmarkierung am nicht präferierten Hangplatz reagierte keines der Versuchstiere in statistisch sicherbarem Maß. Stellte die Bereitschaft zur sozialen Kontaktaufnahme die Hauptmotivation in der Versuchssituation dar, so sollte

man erwarten, daß die Tiere an der Duftmarke interessiert sind, unabhängig davon, auf welchem der beiden Hangplätze sie angebracht ist. Ist dagegen territoriales Verhalten das Hauptmotiv zur Reaktion, so ist verständlich, daß beide männlichen Versuchstiere auf die fremde Geruchsmarke nur am Präferenzplatz reagieren. Das wechselnde Verhalten des zweiten Versuchstieres ergibt sich möglicherweise aus der Identifizierung des Duftdonors und Erinnerungen an aktuelle Vorerfahrungen bezüglich agonistischer Platzkonkurrenzen in der Kolonie.

Aus den Experimenten, in denen die eigene Duftmarke der untersuchten ♂♂ aufgebracht war, läßt sich eine weitere Funktion der olfaktorischen Markierung ersehen. Beide Versuchstiere reagierten durch vermehrte Anwesenheit und häufigeres Aufsuchen des Gitters, wenn ihr Individualgeruch auf dem nicht präferiertem Platz wahrnehmbar war. Aufgeregtes „Hinüberriechen" zum markierten Platz und unruhiges Auf- und Ablaufen auf dem Präferenzplatz zeigten die Erregung der Tiere an. Es war dagegen keine Reaktion zu registrieren, wenn der Präferenzplatz mit dem eigenen Duft markiert war. Die Fledermäuse blieben in diesem Fall völlig ruhig, und es war kein gesteigertes Interesse für den Alternativplatz festzustellen. Dies weist auf die Bedeutung olfaktorischer Markierungen als Orientierungshilfe innerhalb des Ruhequartieres hin. Die offensichtliche Irritation der Tiere, die ihren eigenen Duft an einem Platz wahrnahmen, an dem sie sich kaum aufhielten, zeigt an, daß diese Situation für sie uneindeutig war.

Zusammenfassung

Männliche *Phyllostomus discolor* zeigen ein auffälliges olfaktorisches Markierungsverhalten. Mit charakteristischen Bewegungen des Vorderkörpers wird der präferierte Hangplatz in der Kolonie bzw. die ♀♀ des eigenen Harems mit dem Sekret der Brustdrüse markiert.

In Zweifach-Präferenzwahlen unterschieden ♂ *P. discolor* den eigenen von einem fremden Markierungsduft und reagierten differenziert auf die Gerüche. Der eigene Markierungsduft am Präferenzplatz führte zu keiner Reaktion, wogegen der Duft eines fremden ♂ dort zu einer erhöhten Präsenz führte. Am nicht präferierten Hangplatz dagegen reagierten die Fledermäuse nicht auf den fremden Geruch, erhöhten aber Anflughäufigkeit und Aufenthaltsdauer am markierten Hangplatz, wenn die eigene Markierung dort aufgebracht war.

Die ♀♀ reagierten auf die Markierungsdüfte der ♂♂ nicht durch eine Verschiebung der Platzpräferenzen, sie erhöhten lediglich die Häufigkeit der Anflüge auf die Hangplätze.

Literatur

August, P. V. (1985): Acoustical properties of the distress calls of *Artibeus jamaicensis* and *Phyllostomus hastatus* (Chiroptera: Phyllostomidae). Southwestern Naturalist **30**, 371–375.

Bell, G. P. (1986): Visual acuity, sensitivity and binocularity in a gleaning insectivorous bat, *Macrotus californicus* (Chiroptera: Phyllostomidae). Anim. Behav. **34**, 409–414.

Bilz, R. (1940): Pars pro toto. Ein Beitrag zu Pathologie menschlicher Affekte und Organfunktionen. Leipzig: Thieme.

Bradbury, J. W. (1977): Social Organization and Communikation. In: Biology of Bats. Ed. by W. A. Wimsatt. N.Y.: Academic Press, Bd. III, pp. 2–72.

Bradbury, J. W.; Emmons, L. H. (1974): Social organization of some Trinidad bats. Z. Tierpsychol. **36**, 137–183.

Brown, R. E.; MacDonald, D. W. (1985): The pheromone concept in mammalian chemical communikation. In: Social Odours in Mammals. Ed. by R. E. Brown and D. W. MacDonald. Oxford: Clarendon Press. pp. 1–18.

Buchler, E. R. (1980): Evidence for the use of a scent post by *Myotis lucifugus*. J. Mammalogy **61**, 525–528.

Esser, K.-H.; Schmidt, U. (1989): Mother-Infant Communication in the Lesser Spear-nosed Bat *Phyllostomus discolor* (Chiroptera, Phyllostomidae) – Evidence for Acoustical Learning. Ethology **82**, 156–168.

Fenton, M. B.; Kunz, T. H. (1977): Movements and Bahavior. In: Biology of Bats of the New World family Phyllostomatidae. Part II. Ed by R. J. Baker, J. K. Jr. Jones and D. C. Carter. Lubbock: Spec. Publ. The Museum. Texas Tech. Univ.

Gerell, R.; Lundberg, K. (1985): Social organization in the bat *Pipistrellus pipistrellus*. Behav. Ecol. Sociobiol. **16**, 177–185.

Gustin, M. K.; McCracken, G. F. (1987): Scent recognition between females and pups in the bat *Tadarida brasiliensis mexicana*. Anim. Behav. **35**, 13–19.

Häussler, U.; Nagel, A. (1984): Remarks on seasonal group composition turnover in captive noctules, *Nyctalus noctula* (Schreber, 1774). Myotis **22**, 172.

Kolb, A. (1977): Wie erkennen sich Mutter und Junges des Mausohrs, *Myotis myotis*, bei der Rückkehr vom Jagdflug wieder? Z. Tierpsychol. **44**, 423–431.

Kulzer, E.; Helmy, I.; Necker, G. (1985): Untersuchungen über die Drüsen der Gesichtsregion der Ägyptischen Mausschwanz-Fledermaus *Rhinopoma hardwickei cystops* Thomas, 1903. Z. Säugetierkunde **50**, 57–68.

Laska, M.; Schmidt, U. (1986): Untersuchungen zur olfaktorischen Orientierung bei der Brillenblattnase, *Carollia perspicillata* (Chiroptera). Z. Säugetierkunde, **51**, 129–138.

Laska, M. (1990): Olfactory sensitivity to food odor components in the short-tailed fruit bat, *Carollia perspicillata* (Phyllostomatidae, Chiroptera). J. Comp. Physiol. A **166**, 395–399.

Manske, U.; Schmidt, U. (1976): Visual acuity of the vampire bat, *Desmodus rotundus*, and its dependence upon light intensity. Z. Tierpsychol. **42**, 215–221.

McCracken, G. F.; Bradbury, J. W. (1981): Social organization and kinship in the polygynous bat *Phyllostomus hastatus*. Behav. Ecol. Sociobiol. **8**, 11–34.

Pandey, S. D.; Dominic, C. J. (1987): Gular gland of the Indian Sheath-tailed Bat. Acta Theriol. **32**, 83–93.

Porter, F. L. (1979): Social Behavior in the Leaf-Nosed Bat *Carollia Perspicillata*. II. Social Communication. Z. Tierpsychol. **50**, 1–8.

Schmidt, U.; Schmidt, Ch. (1978): Olfactory thresholds in four microchiropteran bat species. Proceed. Fourth Internat. Bat Research Conf. Ed. by: R. J. Olembo, J. B. Castelino and F. A. Mutere. pp. 7–13.

Schmidt, U.; Höller, P.; Burger, B. (1989): Facial glands in *Miniopterus schreibersi*. In: European Bat Research. Ed. by V. Janàk, I. Horàcek, and J. Gaisler. Praha: Charles Univ. Press. pp. 39–48.

Siegel, S. (1987): Nichtparametrische statistische Methoden. Eschborn: Fachbuchhandlung für Psychologie Verlagsabteilung.

Suthers, R.; Chase, J.; Bradford, B. (1969): Visual form discrimination by echolocating bat. Biol. Bull. **137**, 535–546.

Valdivieso, D.; Tamsitt, J. R. (1964): The histology of the chest gland of the Pale Spear-nosed Bat. J. Mammalogy **45**, 536–539.

Werner, H. J.; Lay, D. M. (1963): Morphologic aspects of the chest gland of the bat *Molossus ater*. J. Mammalogy **44**, 552–555.

Wilkinson, G. S. (1987): Altruism and co-operation in bats. In: Recent advances in the study of bats. Ed. by M. B. Fenton, P. Racey, and J. M. V. Rayner. Cambridge: University Press. pp. 299–323.

Anschriften der Verfasser: Dr. Patrik Höller und Prof. Dr. U. Schmidt, Zoologisches Institut der Rheinischen Friedrich-Wilhelms-Universität Bonn, Poppelsdorfer Schloß, D-53115 Bonn

Z. Säugetierkunde 58 (1993) 266–274

ISSN 0044-3468

Energy intake of captive adult-sized arctic foxes *Alopex lagopus* in Svalbard, in relation to body weight, climate, and activity

By K. Frafjord

Norwegian Polar Research Institute, Oslo, Norway

Receipt of Ms. 26. 10. 1992
Acceptance of Ms. 26. 2. 1993

Abstract

Food intake, change in body weight, and rate of inactivity were studied in two groups of arctic foxes *Alopex lagopus*, caged at Ny-Ålesund on the western coast of Svalbard (79° N). One group consisted of five "tame" foxes held in captivity for 9 to 28 months, and the other group consisted of 20 "wild" foxes held in captivity for 4 to 23 days. Daily energy intake varied between individuals, but no significant seasonal differences were found. Throughout the year mean energy consumption in tame foxes was 623.8 kcal·day^{-1} and in wild foxes 530.2 kcal·day^{-1}. Maintenance requirement was about 120 kcal·kg weight^{-1}·day^{-1}, or 360 kcal·day^{-1} for a 3 kg fox. Yearly mean weight for tame foxes was 3.37 kg, and no seasonal differences in weight were detected. Change in body weight (g/day) was correlated with energy intake (kcal·kg weight^{-1}·day^{-1}) in wild foxes, and for a single tame fox that was caught as an adult. Foxes were generally inactive 60–90 % of the day, with no seasonal differences. Relationships between energy intake, inactivity, and weather (temperature and wind velocity) were weak or absent.

Introduction

The arctic fox *Alopex lagopus* is subject to a highly variable food supply, both within and between years. As a consequence, energy economizing and energy storage should be highly profitable. Underwood (1981) observed that captive foxes fed ad libitum voluntarily reduced their energy intake in winter by a factor of nearly 3 compared to the summer intake, but still maintained a constant body weight. Arctic foxes in captivity may sometimes refuse to eat for several days or weeks (Underwood 1981; Prestrud 1982).

Korhonen (1988a, b) found a seasonal shift in body weight, food intake, and locomotor activity in farm foxes, with a decrease in locomotor activity and an increase in food intake and body weight in the autumn. This trend was reversed during summer. The foxes were most active during the mating period in spring (Korhonen 1988b). Tembrock (1958) and Hilmer and Tembrock (1972) also found that arctic foxes in captivity were most active in the mating period and least active during autumn. Underwood (1981) found no seasonal shifts in body weight of captive foxes in Alaska. The same was found for Svalbard foxes by Prestrud (1982).

Arctic foxes can withstand temperatures below −30 °C without any increase in metabolism (Scholander et al. 1950a; Underwood 1981). This is accomplished by good insulation due to very dense and long winter fur, and possibly to some extent by subcutaneous fat; there is no evidence of an adaptive low body temperature (Scholander et al. 1950b). The growth of fur in arctic foxes parallels annual changes in ambient temperature and photoperiod (Underwood and Reynolds 1980).

In the present study of arctic fox energetics on Svalbard, foxes were held in captivity during the whole year and their body weight, food intake, and activity monitored. The objectives were to verify the seasonal changes in energetics, and to identify factors influencing them.

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5805-0266 $ 02.50/0

Material and methods

Animals

Captive foxes were studied during 1987–1989 at the Research Station of the Norwegian Polar Research Institute in Ny-Ålesund on the western coast of Svalbard (78° 55′ N, 11° 56′ E). Arctic foxes held in captivity were classified into two groups:

1. "Tame" foxes. Five foxes (3 ♂♂, 2 ♀♀) held in captivity for 9 to 28 months. Four of these were caught as pups 1–2 months old, while the fifth was caught when older than 1 year. The pups originated from three different litters, and two were littermates. They were tamed to some extent, and were included in this study from the age of about 5 months, when they were of adult size. One female died during the study (April 1988).
2. "Wild" foxes. Twenty foxes (11 ♂♂, 9 ♀♀) caught primarily in October and November in the vicinity of Ny-Ålesund and caged for 4 to 22 days. Foxes were classified as juveniles (4–12 months) or adults (≥ 1 year) based on the appearance and wear of the canines. The method of trapping is given in Frafjord (1992). Wild foxes were included to examine the possibility that tame foxes may have behaved abnormally and adapted to a long-term and constant supply of food.

Housing

Foxes were held singly in outside cages measuring 2.5 × 2 × 2 m with an earthen floor in summer and a snow floor during other seasons. One wild fox was held in cage measuring 3 × 1 × 1 m elevated 1 m above ground, while another was held in one half of this cage. A wooden box measuring 1.0 × 0.5 × 0.5 m was placed in each cage, and a smaller box was used in the smaller cage. The roof of these boxes was slightly angled, and was a popular resting place for most foxes. In summer, most foxes were also offered a wooden resting shelf, hung up in one corner of the cage. Cages and boxes were cleaned regularly; otherwise disturbances were minimized although the close proximity to Ny-Ålesund made it impossible to exclude all kinds of disturbances. Snow often had to be removed from the cages in winter.

During the second winter, 1988–1989 (mid-November until mid-April), three foxes were housed together inside a building, in a cage measuring 5 × 2 × 1 m (Frafjord 1991). The wall on one side of this building was made of transparent plastic material, and the room was penetrated by winds to a small extent.

Foxes kept outdoors were exposed to natural temperatures and light regime, but wind velocity inside cages was probably slightly lower than outside (as found by Underwood 1981). Foxes could protect themselves against the wind, either by finding shelter inside or behind the nest box, or in a snow cave dug out by themselves. Despite this, most foxes only sought refuge in very bad or rainy weather, and they rested in exposed positions even in strong winds. Foxes kept indoors were exposed to approximate natural light and temperatures, but protected from winds.

Feeding and weighing

Foxes were fed dry fox food (mainly "Ewofox 3", manufactured by Felleskjøpet, Norway) softened in water ad libitum. The daily ration of dry food, amount of water added, and leftovers were weighed to the nearest g (Mettler electronic scale). Since the foxes rarely cached any of this artificial food, all leftovers could be collected daily. The food was prevented from freezing by a small heating element (from September to May). From November 1988 to February 1989, foxes were fed by personnel at the Research Station with less accuracy in weighing, which may have led to a small overestimation of the food intake of the three foxes. Foxes were sometimes kept together in pairs, but these days were excluded from food analysis except for the winter 1988–1989 when mean food intake for the three foxes was calculated. Metabolizable energy content of the food was given by the manufacturer. Water in the form of liquid or snow was provided ad libitum.

Wild foxes were weighed before and after experiments, and otherwise only occasionally. Tame foxes were weighed regularly about each second week, except during January when no fox was weighed. All foxes were weighed before feeding. No drugs were used in the handling of foxes.

Free-living foxes captured and recaptured were weighed to give some information on natural shifts in body weight.

Observations on activity

From September to November 1987, the rate of inactivity (lie + sit + stand) of foxes was observed from a building. All animals were scanned every 5 minutes and their behaviour noted. Most observations were made during the day, but some foxes were observed for 24 hours. Tame foxes were observed for a minimum of 24 hours every second week.

From December 1987 a video camera and time lapse recorder were used to study the inactivity of foxes during 24 hours. Recordings were made about every 2 weeks, including the period when three foxes were kept inside a building, or for a minimum of two 24-hour periods for wild foxes. All recordings from January and most from February were from foxes inside the building. Behaviour was sampled each 5 minutes from the video tapes. A 500 W halogen lamp was used to illuminate the cages during recordings in darkness. The foxes never showed any averse reactions towards this light, and it most likely did not affect their activity.

Food intake, excrementory, and excretory output

One tame and one wild fox were held in a small indoor cage (1.5 × 1 × 1 m) for about a week in winter and spring 1988 for an accurate sampling of food intake and excretory output (the tame fox was used twice). The small size of the cage restricted the activity of these foxes, which was video recorded during at least two 24 hour periods. Foxes were fed as usual, and the faeces produced collected daily. In winter time, the urine could also be collected since it froze instantly. Body weight was recorded daily before feeding without handling the animals, by weighing a small nest box with the fox inside. Also, the room temperature was recorded once daily. The wild fox was used at the end of her captivity, when she was adapted to the artificial food.

Climate

Data on temperature and wind velocity were obtained from the Norwegian Meteorological Institute for the weather station in Ny-Ålesund. Because precipitation is low, less than 400 mm annually (Steffensen 1982), and because these data were incomplete, precipitation was not included in the analysis. To study the joint effect of temperature and wind velocity, a wind chill index (WCI) given by Rosenberg et al. (1983) was calculated (kcal/m^2). Mean monthly temperatures in the region range from −14.0 °C in February to 4.5 °C in July. January and November are the most windy months. The sun is below the horizon from November to February.

Statistics

Results are presented as monthly or seasonal means ± SD between individuals. Analysis of variance (ANOVA) is used to study variation in means. In every ANOVA the individual fox is the sampling unit. Least squares linear regressions are used to study the effect of weather variables on daily energy intake and inactivity. In regression analysis daily energy consumption, percent inactivity, mean temperature, wind speed, or WCI are the sampling units.

Results

Daily food or energy intake in tame foxes was variable, with a maximum range of 87–1390 kcal/day in a single fox, but all ate daily and in no periods refused to eat. Males consumed slightly more kcal/day, weighed more, and were more inactive than females in most months (Fig. 1), but sample size was too small for statistical analysis. Individual variability was great as exemplified by the large standard deviations in figure 1. Seasonal differences (Tab. 1) in energy consumed ($F = 0.05$), weight ($F = 0.21$), and inactivity ($F = 0.74$) were not significant ($p > 0.05$).

Yearly mean energy intake for tame foxes was 620.7 kcal/day. When housed inside during the winter 1988–1989 ($n = 3$), energy intake was comparable to the previous winter (Fig. 1), with a mean of 567.3 kcal/day. Mean weight for all foxes for the whole year was 3.37 kg. Tame foxes were generally inactive 60–90 % of the day (Fig. 1), with a yearly mean of 76.7 %. No consistent relationship between energy intake and body weight was detected for the tame foxes ($r^2 = 0.03–0.19$, $p > 0.05$), except for the male that was caught when more than 1 year old (Fig. 2). The regression slope of this male was not significantly different from the regression slope of wild foxes ($t = 1.87$, $v = 32$, $p > 0.05$).

Most wild foxes adapted rapidly to captive conditions and started to eat at once (most arctic foxes are not very timid to humans), although a few ate only minor amounts of food

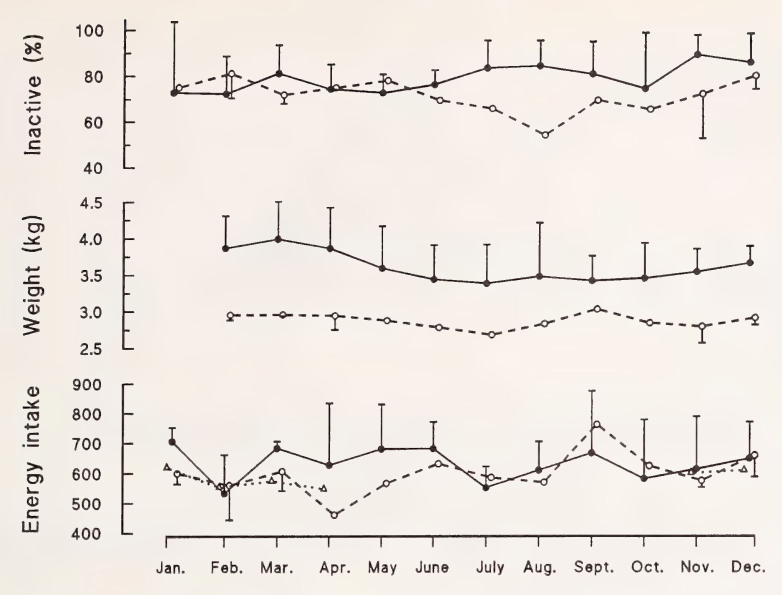


Fig. 1. Monthly mean energy intake (kcal/day), weight, and inactivity of male (●) and female (○) tame arctic foxes during November 1987 through April 1989. 2 males and 1 female were housed collectively during the winter 1988–1989 (△). Only one SD is shown for convenience

and one very fat female probably none at all. Ranges in weight, percent weight change (weight when released in percent of weight at capture), and energy intake were 2.30–4.75 kg, –16.8–37.0 %, and 0–1057 kcal/day, respectively. Several of these wild foxes had a higher energy intake than the tame foxes. Energy intake (F = 0.81), rate of inactivity (F = 0.07), and weight (F = 2.68) (Tab. 2) were not significantly different ($p > 0.05$) from tame foxes in the autumn and winter. Weight changes in wild foxes were significantly correlated

Table 1. **Mean (± SD) daily energy intake (kcal/day), weight (kg), and inactivity (%) in five tame foxes by season**

Spring = April–May, Summer = June–August, Autumn = September–October, Winter = November–March

Sex	Spring	Summer	Autumn	Winter	
		Energy intake			
Males	663.1 ± 142.2	613.4 ± 80.4	614.8 ± 193.9	636.7 ± 96.4	
Females	556.0	598.5	685.2	600.4 ± 61.5	
Combined	636.3 ± 127.9	609.7 ± 66.1	632.4 ± 162.1	622.2 ± 77.4	
		Weight			
Males	3.69 ± 0.54	3.40 ± 0.55	3.43 ± 0.40	3.79 ± 0.35	
Females	2.92	2.76	2.89	2.90 ± 0.10	
Combined	3.50 ± 0.58	3.24 ± 0.55	3.29 ± 0.42	3.43 ± 0.55	
		Inactive			
Males	74.9 ± 8.8	80.2 ± 9.2	75.7 ± 18.8	86.6 ± 9.0	(72.7 ± 15.8)[a]
Females	72.5	62.8	67.2	77.9 ± 2.5	(70.5)[a]
Combined	74.3 ± 7.3	75.9 ± 11.5	73.6 ± 16.0	83.1 ± 8.1	

[a] Second winter in captivity.

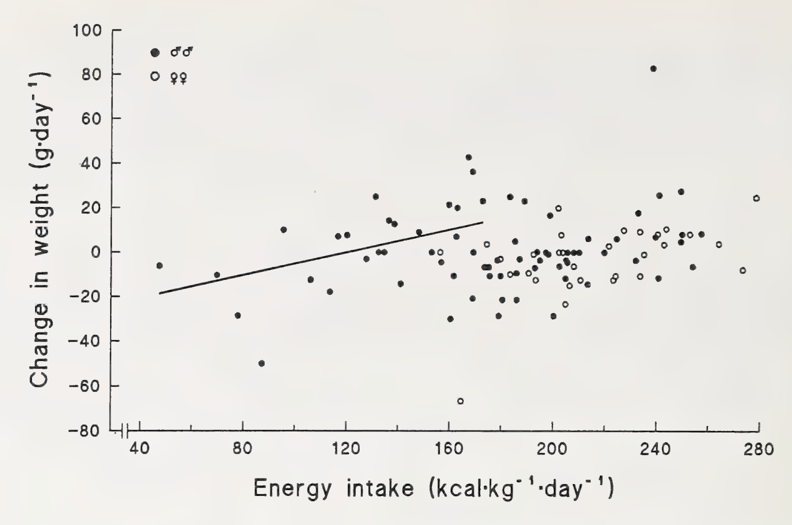


Fig. 2. Relationship between change in weight and energy consumption in five tame foxes during 1987–1988. Mean energy intake for periods between weighing. Regression was significant in one male: $Y = 0.26X - 30.78$, $r^2 = 0.29$, $p < 0.05$

with energy intake (Fig. 3). Minimum energy requirements to maintain weight was 117.9 kcal·kg weight^{-1}·day^{-1} (Fig. 3). The female that did not eat anything lost about 73 g/day. Three wild foxes that were captive in mid-winter (February and March) did not reduce food intake. Mean energy intake of these three foxes (591.1 kcal/day) was not different from wild foxes during September to November ($F = 0.05$, $p > 0.05$). Likewise, their rate of inactivity was not different ($F = 1.17$, $p > 0.05$). Free-living foxes caught and recaptured during the autumn and winter (< 90 days between captures, n = 16) showed a change of 4 g/day in weight. This was only a quarter of the change observed in wild foxes in captivity (mean 15 g/day).

Inspections of scattergrams of energy intake with inactivity, temperature, wind speed, and WCI, and of inactivity with temperature, wind speed, and WCI did not indicate any curvilinear relationships. Thus, linear regressions were used to study these relationships. Regressions for every tame fox were calculated for energy intake with the three weather variables by season and by the whole year (n = 20–328), and for inactivity with energy intake and the three weather variables by the whole year (n = 33–55). Generally, the r^2-values were low (range 0.00–0.15) and no clear patterns (linear relationships) were observed. Two exceptions were found. In one female the relation between energy intake and WCI was high in spring ($r^2 = 0.29$, $p < 0.01$), i.e. 29 % of the variation in energy intake

Table 2. **Mean (±SD) of body weight at capture, number of days in captivity, weight change in % of weight at capture, food intake, and rate of inactivity (n = 19) in 20 wild arctic foxes**

Foxes	n	Body weight (kg)	Days in captivity	Weight change (%)	Food intake (kcal/day)	Inactive (%)
Juvenile ♂♂	7	2.84 ± 0.48	11.0 ± 5.9	12.4 ± 13.1	589.4 ± 244.1	77.3 ± 7.4
Juvenile ♀♀	7	2.99 ± 0.48	9.3 ± 2.5	8.3 ± 15.7	579.5 ± 326.6	74.9 ± 17.7
Adult ♂♂	4	2.95 ± 0.40	10.3 ± 4.5	6.4 ± 8.4	533.4 ± 390.0	81.6 ± 7.3
Adult ♀♀	2	3.75 ± 1.41	9.0 ± 2.8	−13.9 ± 4.2	144.3 ± 204.0	68.3 ± 16.2
All combined	20	3.01 ± 0.59	10.1 ± 4.2	7.2 ± 14.2	530.2 ± 310.7	76.4 ± 12.0

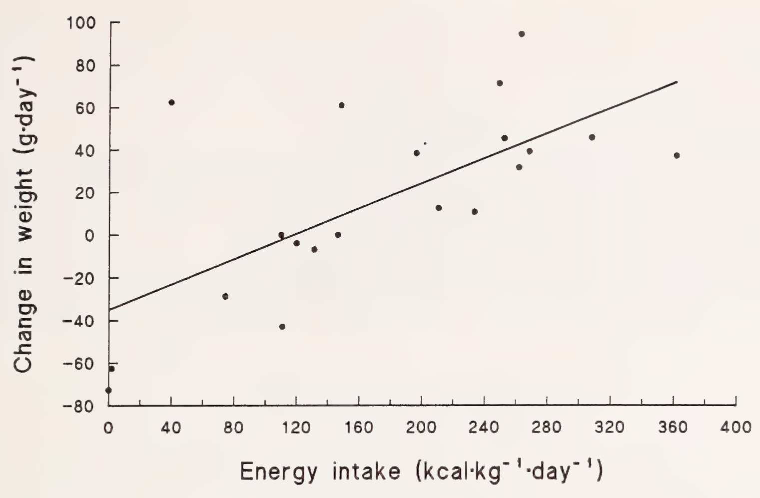


Fig. 3. Relationship between change in weight and energy consumption in 20 wild foxes in the years 1987–1989. Regression line: Y = 0.30X–34.9, $r^2 = 0.46$, $p < 0.01$

was accounted for by variation in WCI. In the other female the relation between energy intake and wind speed was high in winter ($r^2 = 0.36$, $p < 0.05$). Linear regressions of base-10-logarithms of these 5 variables generally did not improve the r^2-values. Among wild foxes energy intake was postively correlated with inactivity ($r^2 = 0.21$, $p < 0.05$), i.e. foxes that were most inactive consumed most food.

The two foxes that were kept in a smaller indoor cage for 3 short periods ate a variable amount of food (Tab. 3). In May, the male was eating more than twice as much as in March, but despite this still lost weight (Tab. 3). Since temperature also had increased significantly, the most likely explanation for "Dick" still loosing weight was an increased level of activity by about 14 %. The female, "Susi", gained only slightly in weight despite eating a fairly large amount of food and being highly inactive (Tab. 3). Mean production of waste (faeces and urine) was about 22 %, and about 78 % of the total energy consumed (energy ingested + fat metabolism) was used for respiration.

Discussion

Underwood's (1981) conclusion that captive arctic foxes in Alaska voluntarily reduced their food intake from 240 kcal·kg $\text{weight}^{-1}\cdot\text{day}^{-1}$ in summer to 85 kcal in winter was not

Table 3. **Food intake, excrementory and excretory output and energy balance in two arctic foxes**

Individual (month)	D	Wt	Wt ch	En in	Feces		Urine		Me	In-act.	Temp.
					kcal	%	kcal	%			
Susi ♀ (March)	7	2.95	14	216.5	50.6	23.4	4.8	2.2	74.4	99.3	−14.5
Dick ♂ (March)	7	3.75	−50	127.7	25.2	19.7	5.1	4.0	76.3	85.0	−18.8
Dick ♂ (May)	9	3.05	−14	279.1	71.7	25.7	–	–	<74.3	71.1	1.7

D = days on experiment, Wt = initial body weight (kg), Wt ch = change in body weight (g/day), En in = energy intake (kcal · kg weight^{-1} · day^{-1}), Me = metabolized energy (%), Inact. = % inactive, Temp. = room temperature (°C). Kcal of faeces und uringe means kcal · kg^{-1} · day^{-1}.

confirmed by the present study on foxes in Svalbard. In contrast, the Svalbard foxes ate a rather constant amount of food all year round. It is unlikely that this resulted from these foxes being more tame or better adapted to captive conditions than the Alaskan ones, because most wild foxes in captivity ate as much as and some even more than the tame foxes. The high food consumption of wild foxes in the autumn and winter indicated that these foxes had not reduced their metabolism or physiologically adjusted themselves to a reduced food availability. Rather, they apparently ate as much as possible and stored the excess energy as body fat, which makes sense for survival during winter time. UNDERWOOD (1971, 1981) gave no explanation of how his foxes could eat less in winter and still maintain body weight. It is unlikely that the large shift in food consumption in his foxes could be explained by foxes more often experiencing lower critical temperatures in the summer than in the winter.

Tame foxes (mean weight 3.37 kg) consumed on average 184.2 and wild foxes (weight 2.91 kg, excluding the single fox that did not eat anything at all) consumed 191.8 $kcal \cdot kg^{-1} \cdot day^{-1}$, which is slightly more than the Alaskan foxes (140.5 $kcal \cdot kg^{-1} \cdot day^{-1}$, weight 4.1 kg, UNDERWOOD 1981). This is approximately 3–3.5 times more than the basal metabolic needs (51.6 $kcal \cdot kg^{-1} \cdot day^{-1}$) (SCHOLANDER et al. 1950b; MCNAB 1989). Minimum energy requirements to maintain body weight were found to be about 120 $kcal \cdot kg^{-1} \cdot day^{-1}$, which is about twice a basal metabolic need of the fox. In addition to basal metabolism and thermoregulation, energy was used in activity, fat deposition, growth of fur, or increase in body size.

The lack of correlation between change in weight and energy consumption among most tame foxes is difficult to explain. Most likely, these foxes often ate more than was strictly needed for maintenance of body weight and utilized the energy less efficiently than what was optimal. In one "tame" fox that was caught as an adult, i.e. more resembling "wild" foxes, a relationship between energy consumption and weight change was found. In a study of red foxes, VOGTSBERGER and BARRETT (1973) calculated the energy loss in faeces to 9%. Energy loss in the present study was about twice as much, which indicates a less efficient utilization of the food, although quality of food would influence this. The correlation between inactivity and energy consumption in wild foxes probably resulted from the least anxious and most relaxed foxes eating most, i.e. foxes that did not adapt as well to captive conditions were more restless and consumed less food. The relations between food intake, inactivity, and weather variables were at best weak. Thus, energy consumption and inactivity were not greatly influenced by weather, probably due to a high insulation value of fox fur (UNDERWOOD 1971, 1981).

Seasonal variation in body weight of tame foxes was not as great as reported by UNDERWOOD (1981). This is in accordance with no seasonal differences in energy consumption and in rate of inactivity. A lowered activity in winter could be beneficial as it will save energy (TEMBROCK 1958; KORHONEN 1988b), but the fox still needs to search actively for food. In the present study, individual differences in yearly inactivity were quite large, as much as 20% in two foxes. Furthermore, one fox was 22% more inactive in his first winter than in the second. Thus, activity of captive foxes fed ad libitum is probably more dependent upon individual differences, housing conditions, and the devlopment of stereotyped movements, than upon an inherent rate of seasonal activity.

The amount of fat in arctic fox carcasses varies seasonally and is highest in the early winter and lowest in spring (UNDERWOOD 1971; PRESTRUD 1982; HAMMILL 1983). Variations in weight during the autumn and winter probably mainly reflect fat deposition or fat catabolism. Fat layers are thickest on the back (UNDERWOOD 1971; PRESTRUD 1982), and may also have some insulative value, especially when the fox is lying in a curled position with its back against the wind. The amount of fat in a wild female that increased in weight from 2.9 to 4.5 kg was estimated as a minimum of 2 kg (44%), which is equivalent to about 19000 kcal (PETERS 1983). If requirements are 120 $kcal \cdot kg^{-1} \cdot day^{-1}$ and mean

weight is set at 3.5 kg, this fat storage would last 45 days. Thus, a fox that is able to deposit a substantial layer of fat may survive 1–2 months without food even at low temperatures during the winter.

Acknowledgements

Analysis of fox food, faeces and urine were made by the Agricultural University of Norway, Department of Animal Husbandry. John H. Vold assisted in building the "fox farm". I also acknowledge Pål Prestrud for assistance in capturing three of the foxes, and for the use of some of his traps. Several employers at the Research Station in Ny-Ålesund assisted in the care of foxes, in snow clearing, and in some video recordings. I would also like to thank Kings Bay Kull Comp. for assistance in building the farm, in snow clearing and for the use of the building "Sibir". I am very indebted to Paul Hinsch, who made the computer program for analysis of activity patterns. Fridtjof Mehlum commented on an earlier draft of this manuscript. This project received a grant from Trygve Gotaas Memorial Fund.

Zusammenfassung

Energieaufnahme bei gefangenen erwachsenen Polarfüchsen (Alopex lagopus) in Spitzbergen. Beziehungen zum Körpergewicht, zum Klima und zur Aktivität

Bestimmt wurden Nahrungsaufnahme, Änderungen des Körpergewichts sowie der Anteil an der Inaktivität bei Polarfüchsen, *Alopex lagopus*, die in Ny-Ålesund an der Westküste Spitzbergens (70° N) in Käfigen gehalten wurden. Eine der untersuchten Gruppen bestand aus fünf „zahmen" Füchsen, die zwischen 9 und 28 Monate in Gefangenschaft gehalten wurden; die zweite Gruppe bestand aus 20 „wilden" Füchsen, die 4 bis 23 Tage gefangen gehalten wurden. Zwischen den Individuen schwankte die tägliche Energieaufnahme, jedoch jahreszeitlich wurden keine signifikanten Unterschiede gefunden. Von den „zahmen" Tieren wurden im Jahresdurchschnitt 623,8 kcal/Tag und von den „wilden" Füchsen 530,2 kcal/Tag aufgenommen. Der Erhaltungsbedarf betrug etwa 129 kcal/kg Gewicht/Tag oder 360 kcal/Tag für einen 3 kg schweren Fuchs. Das mittlere Durchschnittsgewicht der „zahmen" Füchse betrug 3,37 kg, jahreszeitliche Unterschiede gab es nicht. Gewichtsänderungen (g/Tag) konnten mit der Energieaufnahme (kcal/kg Gewicht/Tag) bei den „wilden" Füchsen und für einen einzelnen „zahmen" Fuchs, der als erwachsenes Tier gefangen worden war, bestimmt werden. Für etwa 60–90 % der Tageszeit waren die Tiere inaktiv, saisonale Unterschiede gab es dabei nicht. Beziehungen zwischen der Enenrgieaufnahme, der Inaktivität und dem Wetter (Temperatur und Windgeschwindigkeit) waren entweder nur schwach ausgebildet oder existierten üerhaupt nicht.

References

Frafjord, K. (1991): Bruk av reirkasser hos fjellrev i bur på Svalbard. Norsk Pelsdyrblad **65** (3), 12–14.

— (1992): Size and weight of arctic foxes *Alopex lagopus* from the west Svalbard coast. Polar Record **28**, 68–70.

Hammill, M. O. (1983): The arctic fox, *Alopex lagopus*, as a marine mammal; physical condition and population age structure. M. Sc. Thesis, MacGill University, Montreal.

Hilmer, H. von; Tembrock, G. (1972): Untersuchungen zur circadianen lokomotorischen Aktivitätsperiodik im Jahresgang bei *Vulpes* und *Alopex*. Biol. Zbl. **91**, 443–461.

Korhonen, H. (1988a): Regulation of energy economy in raccoon dogs and blue foxes: A process of dynamic interactions. Comp. Biochem. Physiol. **91A**, 263–268.

— (1988b): Seasonal changes in activity and behavioural patterns of farm-raised foxes (*Alopex lagopus*). Scientifur **12**, 21–26.

Mcnab, B. K. (1989): Basal rate of metabolism, body size, and food habits in the order Carnivora. In: Carnivore behavior, ecology, and evolution. Ed. by J. L. Gittleman. London: Chapman and Hall. Pp. 335–354.

Peters, R. H. (1983): The ecological implications of body size. Cambridge: Cambridge University Press.

Prestrud, P. (1982): Årstidsvariasjoner i basalmetabolisme og fettlagring hos fjellreven (*Alopex lagopus* L.) på Svalbard. University of Oslo, Oslo. Cand. real. thesis.

Rosenberg, N. J.; Blad, B. L.; Verma, S. B. (1983): Microclimate, the biological environment. New York: John Wiley and Sons.

Scholander, P. F.; Hock, R.; Walters, V.; Irving, L. (1950b): Adaptation to cold in arctic and tropical mammals and birds in relation to body temperature, insulation and basal metabolic rate. Biol. Bull. **99**, 259–271.

SCHOLANDER, P. F.; HOCK, R.; WALTERS, V.; JOHNSON, F.; IRVING, L. (1950a): Heat regulation in some arctic and tropical mammals and birds. Biol. Bull. **99**, 237–258.

STEFFENSEN, E. L. (1982): The climate at Norwegian arctic stations. Klima **5**, 3–14.

TEMBROCK, G. (1958): Zur Aktivitätsperiodik bei *Vulpes* und *Alopex*. Zool. Jb. Physiol. **68**, 297–324.

UNDERWOOD, L. S. (1971): The bioenergetics in the arctic fox (*Alopex lagopus*). Ph. D. Thesis, Pennsylvania State Univ.

— (1981): Seasonal energy requirements of the arctic fox (*Alopex lagopus*). In: Worldwide Furbearer Conf. Proc., Frostburg, Aug. 3–11, 1980. Ed. by J. A. CHAPMAN and D. PURSLEY. Pp. 368–385.

— REYNOLDS, P. (1980): Photoperiod and fur lengths in the arctic fox (*Alopex lagopus* L.). Int. J. Biometeor. **24**, 39–48.

VOGTSBERGER, L. M.; BARRETT, G. W. (1973): Bioenergetics of captive red foxes. J. wildl. Manage. **37**, 495–500.

Author's address: KARL FRAFJORD, Museum of Zoology, University of Bergen, Muséplass 3, N-5007 Bergen, Norway

Z. Säugetierkunde 58 (1993) 275–280

ISSN 0044-3468

Régime alimentaire de la fouine *(Martes foina)* durant un cycle de pullulation du campagnol terrestre *(Arvicola terrestris scherman)* dans le Jura suisse

Par Nicole Lachat Feller

Institut de Zoologie, Université de Neuchâtel, Neuchâtel, Suisse

Réception du Ms. 27. 12. 1992
Acceptation du Ms. 22. 3. 1993

Abstract

Diet of the Stone marten (Martes foina) during a population peak of the water vole (Arvicola terrestris scherman) in the Swiss Jura

Investigated the diet of the stone marten *(Martes foina)* in the Swiss Jura in relation to water vole abundance. 850 scats were collected and analyzed from March 1987 to November 1991. Changes of the diet were compared to the general diet, studied between two population peaks. Significant differences were shown. Mammals were the main prey, representing 37.9 % of all items (N = 1181). Simultaneously the number of water voles, recorded by other authors in the same area, was noted.

The diet changed from year to year, following the level of water vole population. At the top of the peak, water voles were present in 90.4 % of the scats. Stone marten is enhanced as an opportunistic predator whose impact on the water vole population is discussed.

Introduction

Le régime alimentaire général de la fouine a déjà été étudié sur le même terrain (Marchesi et al. 1989). Par la suite, il a paru important de définir plus précisément l'importance que prend le campagnol terrestre *(Arvicola terrestris scherman)* dans ce régime. Ce rongeur montre de fortes fluctuations périodiques de ses populations dans cette région (Saucy 1988). Debrot (1981, 1983) et Erlinge (1981) ont montré que ces pullulations ont une grande influence sur l'hermine *(Mustela erminea)*. Il était dès lors intéressant de savoir si c'était aussi le cas pour un autre mustélidé comme la fouine, d'autant plus que Waechter (1975) y fait allusion en ce qui concerne certaines populations de fouines en Alsace (France).

Matériel et méthodes

L'étude est réalisée dans le Jura suisse, à environ 30 km au nord de Neuchâtel (47°09′ N, 6°56′ E). Ce terrain, aux paysages cloisonnés par de nombreuses haies et par des murs de pierres sèches, a été décrit par Marchesi et al. (1989). La fouine y trouve aisément des gîtes confortables et des zones de chasse où les proies sont abondantes.

L'analyse des crottes est réalisée selon les méthodes mises au point par Debrot et al. (1982) et Marchesi et Mermod (1989).

Les crottes ont été collectées sur une période allant de mars 1987 à novembre 1991 inclus.

La récolte est faite à chaque début de saison, le plus souvent dans des bâtisses rurales qui constituent les gîtes de prédilection des fouines dans cette région. Simultanément, les populations de campagnols terrestres ont été recensées, sur le même terrain, à raison de 3 piègeages annuels (Weber et Aubry 1993).

Le calcul de la niche alimentaire (BS) se fait selon la formule de Hespenheide (1975), déjà utilisée par Marchesi et al. (1989).

Résultats

Régime alimentaire

Le régime alimentaire général de la fouine en période de faible densité de campagnol terrestre avait été déterminé par l'analyse de 580 crottes, récoltées entre juin 1985 et février 1987, soit entre deux pullulations de ce rongeur (Marchesi et al. 1989). Depuis, 850 crottes ont été analysées sur une période d'environ 5 ans (mars 1987–novembre 1991), soit durant un cycle complet de pullulation du campagnol.

Si la fouine consomme toujours une grande variété de nourriture (animale ou végétale), son régime diffère significativement de celui établi hors de la pullulation (Fig. 1) (chi^2 = 96,24; $p < 0,001$).

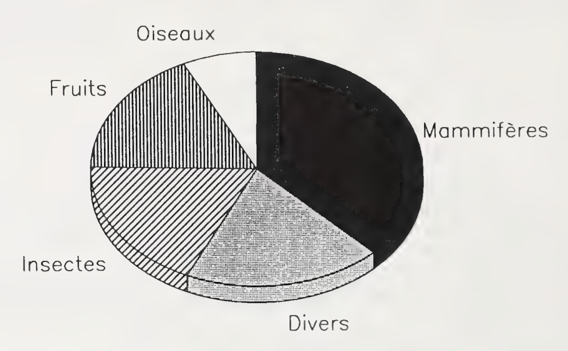


Fig. 1. Régime alimentaire de la fouine lors d'une pullulation d'*Arvicola terrestris*. Distribution des catégories de proies. (N = 1181)

Cette différence se marque surtout par la supplantation des fruits par les mammifères qui prennent la première place dans le régime avec 37,9 % (N = 1181) des items analysés. Il s'agit à 77,9 % (N = 448) de campagnols terrestres, *Arvicola terrestris.* Les autres micromammifères, tels que *Apodemus* spp., *Clethrionomys glareolus, Pitymys* spp. ou *Microtus* spp. sont nettement plus rares.

Les fruits (17,7 %) accusent une forte baisse due à la réorientation du régime et n'arrivent plus qu'en quatrième position.

Les «divers» (19,2 %) et les insectes (18,1 %), de même que les oiseaux (7,1 %) se maintiennent à peu près à leur niveau antérieur.

Variations annuelles du régime

En considérant le régime alimentaire de la fouine année par année, durant tout le cycle de pullulation du campagnol, on constate des variations significatives (Fig. 2).

1987: dès le début de la pullulation, les mammifères prennent la première place avec 38 % des proies analysées (N = 463; chi^2 = 35,57; $p < 0,001$). 42,1 % des crottes (N = 397) contiennent des restes de mammifères (27,7 % contiennent des restes de campagnol terrestre) (Fig. 3). La proportion de campagnol terrestre dans les crottes «avec poils» est de 65,8 % (N = 167). L'importance des fruits (11,9 %) est significativement diminuée (chi^2 = 75,79; $p < 0,001$).

1988: la densité des populations de campagnols augmente considérablement et la progression des mammifères dans le régime se poursuit, avec 51,3 % des proies (N = 152; chi^2 = 7,81; $p < 0,01$). 79,2 % des crottes (N = 96) contiennent des poils (67,7 % contiennent du campagnol) (Fig. 3). La proportion d'*Arvicola terrestris* dans les crottes «avec poils» est de 85,5 % (N = 76). La diminution des fruits se confirme (12,5 %).

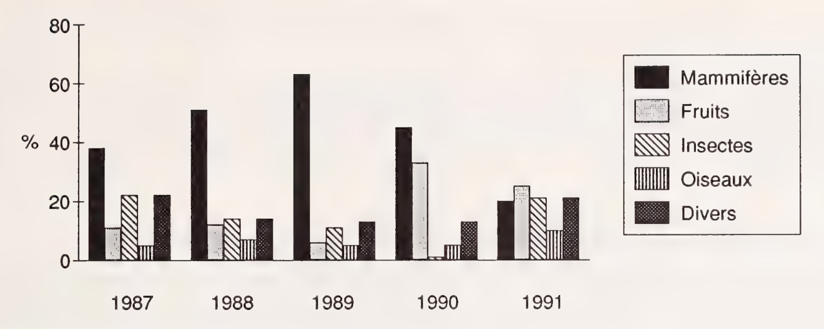


Fig. 2. Variations annuelles des catégories de proies. Pourcentages absolus. (N 87 = 463) (N 88 = 152) (N 89 = 107) (N 90 = 130) (N 91 = 329)

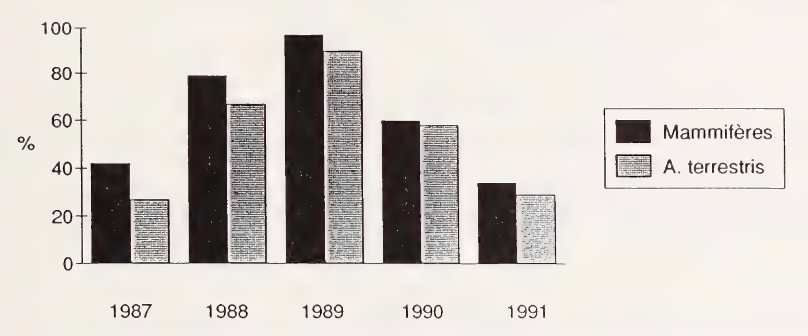


Fig. 3. Proportions de crottes contenant des poils. (Mammifères/*Arvicola terrestris*)

Toutefois, il n'y a pas de baisse significative par rapport à 1987 (chi^2 = 0,004; p > 0,05). Ce sont surtout les catégories insectes et «divers» qui diminuent.

1989: au plus fort de la pullulation, les mammifères représentent le 63,6 % des proies (N = 107). L'augmentation n'est toutefois pas significative par rapport à 1988 (chi^2 = 3,34; p > 0,05). 97 % des crottes (N = 63) contiennent des poils (90,4 % contiennent du campagnol) (Fig. 3). La proportion d'*Arvicola terrestris* dans les crottes «aves poils» est de 93,4 % (N = 61).

Les fruits accusent une baisse importante bien que non significative par rapport à 1988 (chi^2 = 1,85; p > 0,05), avec 6,5 % des items analysés. Les insectes et les oiseaux diminuent également.

1990: le cycle de pullulation est en phase descendante. La tendance s'inverse. Les mammifères chutent de façon significative (45,4 %; N = 130; chi^2 = 7,07; p < 0,01), alors que l'importance des fruits s'accroît considérablement en comparaison avec 1989 (33,9 %; chi^2 = 24,31; p < 0,001).

60 % des crottes (N = 97) seulement contiennent encore des poils (58,8 % contiennent du campagnol) (Fig. 3). Par contre, la proportion d'*Arvicola terrestris* augmente toujours dans les crottes «avec poils», pour culminer à 98,3 % (N = 58).

Il est intéressant de noter que les insectes chutent également de façon significative (1,5 %; chi^2 = 8,22; p < 0,01).

1991: la densité des populations de campagnols continue à diminuer durant le printemps et l'été. En automne, c'est l'effondrement.

Dans le régime, les mammifères ont retrouvé leur importance d'avant la pullulation (20,4 %, N = 329), suite à une nouvelle baisse significative (chi^2 = 28,04; p < 0,001). Seuls 34 % des crottes (N = 197) contiennent encore des poils (29,4 % contiennent du

campagnol) (Fig. 3). *Arvicola terrestris* reste la proie mammifère la plus chassée, avec 86,6 % (N = 67) des items analysés.

Les analyses de crottes s'arrêtent en novembre 1991. Les crottes de l'hiver (décembre 91–février 92) ne sont pas prises en considération. Ceci explique l'importance un peu minimisée affichée par les fruits. L'augmentation des oiseaux n'est pas significative (chi^2 = 2,49; $p > 0,05$).

Relation entre consommation et densité du campagnol terrestre

Les moyennes annuelles de densité du campagnol, établies à partir des données récoltées par Weber et Aubry (1993) sont les suivantes: 1987: pas de données; 1988: 590 campagnols/ha; 1989: 620 campagnols/ha; 1990: 443 campagnols/ha; 1991: 123 campagnols/ha.

Elles ont permis de montrer qu'il existe une corrélation significative entre l'abondance de ces rongeurs durant les cinq années du cycle et leur consommation par la fouine (coefficient de corrélation de Spearman, r = 0,94, p = 0,005).

Niche alimentaire

La niche alimentaire (BS) calculée à partir des cinq catégories de proies valait 0,8058 pour la période hors pullulation (Marchesi et al. 1989).

Les valeurs durant la pullulation de campagnols se montent à: 1987: 0,7041; 1988: 0,5192; 1989: 0,3181; 1990: 0,4799; 1991: 0,9286.

Discussion

La fouine est bien connue comme étant une généraliste et de surcroît une opportuniste (Waechter 1975; Delibes 1978; Kalpers 1983). Elle exploite d'abord les ressources les plus abondantes et les plus aisément accessibles. Son régime peut dès lors subir des variations qui sont autant de spécialisations locales ou temporelles (Marchesi et al. 1989).

Dès le début de la pullulation de campagnols, son régime se réoriente, les mammifères prenant la première place, au détriment des fruits.

Conformément à la théorie de l' «optimal foraging» (Emlen 1966; Schoener 1971; Pyke 1977) un prédateur devrait augmenter sa sélectivité sur les proies préférées lorsque celles-ci augmentent en densité. Il devrait maximiser la différence entre les gains et les coûts de sa chasse et décider quelles proies (ou types de proies) seront les plus favorables (Pianka 1974; Mac Arthur 1972; réf in Erlinge 1981). Ce sont les proies fournissant le plus d'énergie qui seront préférées. C'est ce qui se produit avec le campagnol terrestre. Etant le plus abondant et le plus gros micromammifère à disposition dans notre région, il devient la proie principale. Dès lors, la niche alimentaire de la fouine se réduit considérablement pour prendre, au sommet de la pullulation, une valeur se rapprochant de celle d'une niche de spécialiste, telle que l'hermine (Debrot 1981). On constate d'ailleurs, en accord avec Erlinge (1981) que la largeur de la niche est inversement proportionnelle à la densité de campagnols.

Lorsque la population de campagnols chute (1990), on assiste à une brusque remontée des fruits suivie l'année suivante par un étalement de la niche alimentaire. Il semblerait que la fouine connaît une certaine période de flottement durant laquelle son régime doit se réajuster afin de pallier à la diminution des proies-mammifères. En bonne généraliste euryphage, elle consomme alors un large éventail de proies, accentuant sa pression sur des proies normalement de moindre importance ou d'intérêt secondaire. Elle réduit sa dépendance vis-à-vis du campagnol en exploitant le plus efficacement possible toutes les autres sources de nourriture ce qui explique la valeur très élevée de la niche alimentaire durant cette période.

L'impact de la fouine en tant que prédateur du campagnol terrestre n'est pas facile à estimer.

Plusieurs auteurs (KREBS 1974; ERLINGE 1975; ANDERSSON et ERLINGE 1977) s'accordent à dire que la prédation ne saurait suffire à stopper une pullulation en phase ascendante. Selon ces auteurs, les prédateurs (toutes espèces confondues) ne peuvent que réduire les pics de pullulation, donc maintenir les populations à un niveau inférieur et retarder le prochain pic.

La phase descendante de la pullulation se déclencherait également indépendamment des prédateurs qui ne joueraient un rôle réel qu'en fin de pullulation, accélérant la chute.

Sur notre terrain, la fouine joue certainement ce rôle de modérateur, en compagnie du renard *(Vulpes vulpes)*, du chat domestique *(Felis catus)* et du hibou moyen-duc *(Asio otus)*.

Son impact est probablement important au moment de l'effondrement des populations. On en veut pour preuve la proportion importante de campagnols terrestres trouvée dans les crottes contenant des poils en 1990 (près de 100 % des proies-mammifères) et jusqu'en 1991 (plus de 86 %).

Toujours selon les théories scandinaves (ERLINGE et al. 1984), la présence de généralistes en nombre suffisant et stable (grâce à des proies alternatives) devrait prévenir les pullulations car ils réagissent promptement aux changements de densité des micromammifères. Ceci n'est pas du tout vérifié sur notre terrain malgré une densité importante de prédateurs (chats, renards, fouines).

Il est vrai toutefois que si les populations de chats et de fouines semblent se maintenir au fil des années, ce n'est pas le cas pour le renard (WEBER et al. 1991). Les populations de ce canidé fluctuent rapidement, notamment à cause de la pression de la chasse.

Une étude à plus long terme serait nécessaire pour tenter d'expliquer l'existence de pullulations du campagnol terrestre malgré la présence d'un nombre important de prédateurs, ceci d'autant plus que ces pullulations semblent être différentes de celles des autres micromammifères (SAUCY 1988).

Remerciements

Ce travail fait partie d'une thèse de doctorat effectuée sous la direction du Prof. C. MERMOD que j'aimerais remercier ici pour son soutien et pour avoir bien voulu relire ce manuscrit.

Ma reconnaissance va d'autre part à toutes les personnes qui, d'une manière ou d'une autre, ont permis la réalisation de ce travail et plus particulièrement au Dr P. MARCHESI pour ses commentaires sur le texte, à Mme JACQUELINE MORET pour ses conseils en statistiques, à mes collègues et à tout le personnel de l'Institut de Zoologie ainsi qu'aux paysans de La Chaux d'Abel/Mont-Soleil.

Résumé

La stratégie alimentaire de la fouine *(Martes foina)* a été étudiée durant un cycle complet de pullulation du campagnol terrestre (*Arvicola terrestris scherman*). 850 crottes ont été récoltées et analysées sur une période allant de mars 1987 à novembre 1991. Les fluctuations de ce régime sont comparées au régime de base de la fouine, établi en dehors d'une période de pullulation de campagnols.

Des différences significatives sont mises en évidence: les mammifères prennent la première place, avec 37,9 % (N = 1181) des items analysés. Les fruits perdent une grande partie de leur importance. Les autres catégories (insectes, oiseaux, divers) conservent à peu près leur niveau d'avant la pullulation.

Il existe une corrélation significative entre l'abondance des campagnols et leur consommation par la fouine.

Zusammenfassung

Nahrungsspektrum beim Steinmarder (Martes foina) während einer zyklischen Vermehrung der Schermaus (Arvicola terrestris scherman) im Schweizer Jura

Das Nahrungsspektrum des Steinmarders *(Martes foina)* wurde in Zeiten rascher zyklischer Vermehrung der Schermaus *(Arvicola terrestris scherman)* untersucht. 850 Kotballen wurden seit März 1987 bis November 1991 gesammelt und analysiert. Das Nahrungsspektrum während der zyklischen

Vermehrung der Schermaus wurde mit dem Spektrum außerhalb solcher Massenvermehrungen verglichen.

Kennzeichnend gilt: Steinmarder fressen hauptsächlich Kleinsäuger (37,9 % der Proben, N = 1181). Früchte scheinen weniger wichtig. Andere Beutegruppen (Insekten, Vögel, andere) bleiben ungefähr gleich.

Es besteht eine enge Wechselbeziehung zwischen dem Schermaus-Angebot und dessen Nutzung durch Steinmarder.

Références

Andersson, M.; Erlinge, S. (1977): Influence of predation on rodent populations. Oikos **29**, 591–597.

Debrot, S. (1981): Trophic relations between the stoat *(Mustela erminea)* and its prey, mainly the water vole *(Arvicola terrestris scherman)*. In: Worldwide Furbearer Conf. Proc. Ed. by J. A. Chapman and D. Pursley. Frostburg, Maryland, August 1980. Vol. **2**, 1259–1289.

Debrot, S.; Fivaz, G.; Mermod, C.; Weber, J. M. (1982): Atlas des poils de mammifères d'Europe. Neuchâtel: Institut de Zoologie.

Debrot, S. (1983): Fluctuations de populations chez l'hermine *(Mustela erminea)*. Mammalia **47**, 323–332.

Delibes, M. (1978): Feeding habits of the stone marten, *Martes foina* (Erxleben, 1777) in Northern Burgos, Spain. Z. Säugetierkunde **43**, 282–288.

Emlen, J. M. (1966): The role of time and energy in food preference. Am. Nat. **100**, 611–617.

Erlinge, S. (1975): Predation as a control factor of small rodent populations. In: Biocontrol of rodents. Ed. by L. Hansson and B. Nilsson. Stockholm: Swedish Natural Science Research Council. Pp. 195–199.

Erlinge, S. (1981): Food preference, optimal diet and reproductive output in stoats *Mustela erminea* in Sweden. Oikos **36**, 303–315.

Erlinge, S. (1984): Can vertebrate predators regulate their prey? Am. Nat. **123**, 125–133.

Hespenheide, M. A. (1975): Prey characteristics and predator niche width. In: Ecology and Evolution of Communities. Ed. by M. L. Cody and J. M. Diamond. Cambridge, Mass.: Harvard Univ. Press. Pp. 158–180.

Kalpers, J. (1983): Contribution à l'étude écoéthologique de la fouine *(Martes foina)*: stratégie d'utilisation du domaine vital et des ressources alimentaires. I. Introduction générale et analyse du régime alimentaire. Cahiers Ethol. appl. **3**, 145–163.

Krebs, C. J.; Myers, J. H. (1974): Population cycles in small mammals. In: Advances in Ecological Research. Ed. by Mac Fayden. New York, London: Academic Press. Vol. **8**, 267–399.

Marchesi, P.; Mermod, C. (1989): Régime alimentaire de la martre (*Martes martes* L.) dans le Jura suisse (Mammalia: Mustelidae). Revue suisse Zool. **96**, 127–146.

Marchesi, P.; Lachat, N.; Lienhard, R.; Debieve, P.; Mermod, C. (1989): Comparaison des régimes alimentaires de la fouine (*Martes foina* Erxl.) et de la martre (*Martes martes* L.) dans une région du Jura suisse. Revue suisse Zool. **96**, 281–296.

Pyke, G. H.; Pulliam, H. R.; Charnov, E. L. (1977): Optimal foraging: A selective review of theory and tests. Quart. Rev. Biol. **52**, 137–154.

Saucy, F. (1988): Dynamique de population, dispersion et organisation sociale de la forme fouisseuse du campagnol terrestre (*Arvicola terrestris scherman* [Shaw], Mammalia, Rodentia). Thèse de doctorat, Univ. Neuchâtel.

Schoener, T. W. (1971): Theory of feeding strategies. Ann. Rev. Ecol. Syst. **2**, 369–404.

Waechter, A. (1975): Ecologie de la fouine en Alsace. Terre et Vie **29**, 399–457.

Weber, J. M.; Aubry, S.; Lachat, N.; Meia, J. S.; Mermod, C.; Paratte, A. (1991): Fluctuations and behaviour of foxes determined by nightlighting. Preliminary results. Acta Theriologica **36**, 285–291.

Weber, J. M.; Aubry, S. (1993): Predation by foxes, *Vulpes vulpes*, on the fossorial form of the water vole, *Arvicola terrestris scherman*, in western Switzerland. J. Zool. **229**, 553–559.

Adresse de l'auteur: Nicole Lachat Feller, Institut de Zoologie, Université de Neuchâtel, Chantemerle 22, CH-2007 Neuchâtel, Suisse

Z. Säugetierkunde 58 (1993) 281–285

ISSN 0044-3468

Activity of the Yellow mongoose *Cynictis penicillata* in a coastal area

By P. Cavallini

Department of Zoology, John Ellerman Museum, University of Stellenbosch, Stellenbosch, South Africa

Receipt of Ms. 25. 9. 1992
Acceptance of Ms. 27. 12. 1992

Abstract

Observed the activity of yellow mongooses (*Cynictis penicillata*) in the West Coast National Park, Cape Province, South Africa. The majority of the population was captured, and a sample (4 females; 3 males) was radio-tracked. Radio-collared mongooses were usually (86 % of time) involved in the same kind of activity as uncollared ones. Mongooses spent most of the day (37 % of radiolocations) foraging. Time of start and cessation of activity was correlated to sunset and sunrise times, minimum and maximum temperature, windspeed, and meteorological conditions (mist, rain, cloudiness). The availability of insects may be a factor underlying this relation. This can explain the differences in activity rhythms among previous studies. Total size of home range (minimum convex polygon) used each day, percentage of total home range used each day, and total daily movements were not related to any of the above variables.

Introduction

The yellow mongoose *Cynictis penicillata* (Carnivora: Herpestidae) feeds mostly on insects, but also rodents are frequently eaten. It frequents open areas and lives singly or in small groups, spending the night and part of the day in burrows (Skinner and Smithers 1990; Cavallini 1993). Gravid females have been recorded from mid-July to the end of December (Zumpt 1969).

In spite of its abundance (Stuart 1981) and apparently diurnal habits, data on the activity budget of this species are scarce. Earlé (1981) reported a marked effect of temperature on the activity of *C. penicillata*, but presented no supporting data. This study investigates the activity budget and ranging movements of the yellow mongoose in relation to selected meteoreological variables.

Material and methods

The study was conducted in the West Coast National Park (2700 ha), Cape Province, South Africa. The climate is mediterranean and rainfall is concentrated in winter. Over 80 % of the area is covered by bush, the rest being covered by short grass. Further details on habitat are reported by Boucher and Jarman (1977) and Cavallini and Nel (1990).

Twelve yellow mongooses were captured and marked. For trapping and radiotracking methodologies, see Cavallini (1993). From 4 to 7 unmarked mongooses were observed in the area. Total population size was therefore estimated at 16–19 individuals. Of these, seven adult mongooses (4 females; 3 males; 37 % to 44 % of total population) were radio-tracked from March to May 1991, one animal per day, randomly chosen. The non-breeding season was selected to avoid the eventual effects of rutting activities on the time budget. Since preliminary observations in the area and a review of the literature (e. g. Herzig-Straschil 1977) suggested that yellow mongooses left the den after sunrise, retreating back into the den at sunset, they were tracked from before sunrise (06.30–07.00 h) until after sunset (19.00 h–19.30 h), and all mongooses within sight were observed. The eventual occurrence of nocturnal activity was checked during ten nights. During a random period, all radio-equipped animals were located and activity was checked for 15 min through signal intensity fluctuations. The exact location of the mongoose (inside or outside a den) was then checked by

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5805-0281 $ 02.50/0

homing on the signal, while still checking for the constancy of signal. This procedure assured that the mongoose did not change location (e. g. retreating into the den) while I approached it.

Definitions

Behavioural variables

Start of activity: the time either of first movement > 50 m from the den or beginning of feeding (whichever came first). Yellow mongooses are known to rest ('sunbathing') outside the den in the morning, before beginning to feed and travel (EARLÉ 1981).

Stop of activity: stop of feeding or proximity (< 50 m) to the den (whichever came last).

Daily home range size: total size of the minimum convex polygon (HAYNE 1949) enclosing all locations of a particular animal on a day. Although not an ideal technique, the minimum convex polygon was found to perform better than more recent methods in this case (CAVALLINI 1993). In fact, the minimum convex polygon is less sensitive to the use of autocorrelated data, as those used in the present study (SWIHART and SLADE 1985).

Percentage of total range: percentage of daily home range size on total minimum convex polygon enclosing all the locations recorded for a particular animal.

Daily movements: sum of all distances between consecutive 15-min fixes recorded on one day.

Number of active fixes: the total number of locations in which the radio-tracked mongoose was active during the day.

Meteorological variables

Minimum and maximum daily shade temperatures: measured at about 20 cm from the ground, with a Brannan dry-bulb thermometer.

Average windspeed: measured with an anemometer at 2 m from the ground (windspeed was measured in m/s every hour during the day, then averaged and converted to a Beaufort scale).

Weather conditions: 1 = clear sky for more than 80 % of the day; 2 = variable; 3 = cloudy for more than 80 % of the day; 4 = rain.

Morning fog: duration, starting from 06.30 h until complete dissolvence of fog.

Standard tables were used for sunrise and sunset times.

Standard nonparametric tests (SIEGEL 1956) were used. Because of large number of tests, significance level was set at 0.01 (RICE 1989). When the analysis of variance showed no significant differences (conservatively, I used $P > 0.1$) among individuals, data were pooled (because of repeated measures on the same individuals, these analyses should not be considered a rigorous statistical testing, but rather as an indication to be tested with a larger data base). Otherwise, analyses were done separately for each individual.

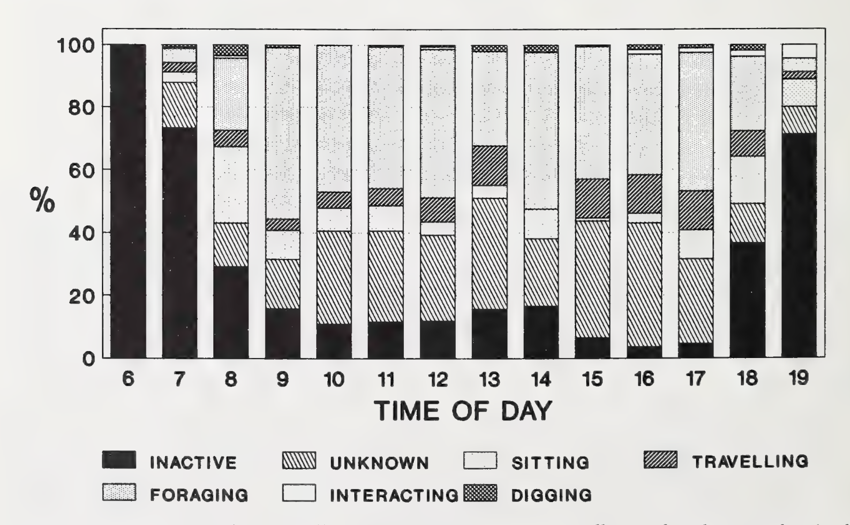


Fig. 1. Activity budget of seven yellow mongooses *Cynictis penicillata* (4 females; 3 males) in the West Coast National Park in relation to time of day, during March-May 1991 (n = 2260)

Results

During the study, minimum temperatures ranged between 8 °C and 23 °C, and maximum between 18 °C and 35 °C. Windspeed reached 5 on only one day; the mode was 2. Most tracking days (56.5 %) were clear. Rain occurred on 8.9 % of tracking days, and fog on 32.6 %, lasting an average of 107 min when present. The sun rose between 06.48 h and 07.31 h, and set between 19.05 h and 17.57 h. A total of 2260 daytime animal locations was obtained (range: 119–489 per individual). Mongooses were never seen outside the den when tracking periods started, and were already in the den from ≥ 30 min when observations ended. Mongooses spent most of day (37.2 % of fixes), foraging, especially from 09.00 h to 18.00 h, without an evident peak in this activity. They sat and groomed in 8.4 % of fixes (particularly around 08.00 h and 18.00 h), and travelled in 7.4 %, mostly between 13.00 h and 18.00 h. Occasionally (26.8 % of days), they rested inside the den at mid-day, for up to 4.5 hours. Social interactions (0.8 % of fixes) were most frequent in late evening, especially before entering the den. Digging at the den (opening new holes and enlarging old ones) occurred in 1.1 % of fixes, particularly in the morning (08.00 h), at mid-day (13.00 h–14.00 h) and in the evening (16.00 h–18.00 h). They were not visible for 24.9 % of fixes (Fig. 1). Night-time fixes revealed no activity. Mongooses were invariably found in den during the night. When untagged mongooses were observed, they were often (86.3 % of sightings) seen involved in the same kind of activity at the same time as the tagged ones. Mongooses started their daily

Average and individual differences for seven behavioural variables of seven yellow mongooses *Cynictis penicillata* (4 females; 3 males) in the West Coast National Park, during March–May 1991

Correlations with metereological variables (Spearman rank correlation) are reported. For definition of variables, see 'Material and methods'

Behavioural variable	Average ± S.D.	Kruskall-Wallis ANOVA	Correlated metereological variables
Start of activity	08.45 h ± 74 min	H = 9.82, d.f. = 6, P = 0.13	Sunrise time, mist hours, weather; $r_s > 0.42$, $P < 0.001$, n = 69
Stop of activity	18.15 h ± 35 min	H = 5.04, d.f. = 6, P = 0.40	Sunset time, max temperature, windspeed; $r_s > 0.33$, $P < 0.01$, n = 69
Mid-day rest hours	10 ± 50 min	H = 7.49, d.f. = 6, P = 0.27	Maximum temperature; $r_s = 0.59$, $P < 0.001$, n = 69
N of active fixes	39.3 ± 5.0	H = 14.50, d.f. = 6, P = 0.024; Among males: H = 0.60, d.f. = 2, P = 0.738; Among females: H = 13.58, d.f. = 3, P = 0.022;	Males (pooled): mist hours; $r_s = -0.55$, P = 0.016, n = 27. Daylength; $r_s = 0.65$, $P < 0.01$, n = 27 Females (individually): none ($r_s < 0.37$, $P > 0.3$, $14 > n > 8$)
Daily range	20.8 ± 21.5 ha	H = 32.05, d.f. = 6, P < 0.001	None ($r_s < 0.47$, $P > 0.16$, $15 > n > 8$)
Percentage of total range	33.2 ± 16.8 %	H = 2.97, d.f. = 6, P > 0.5	None ($r_s < 0.19$, $P > 0.18$, n = 69)
Total movements	3229 ± 1135 m	H = 23.54, d.f. = 6, P < 0.001	None ($r_s < 0.59$, $P > 0.15$, $15 > n > 8$)

activity between 07.15 h and 12.00 h, and stopped between 16.30 h and 19.15 h, with no significant individual differences (for all significance levels mentioned, see table). Time of start of activity was positively correlated to sunrise time, mist hours, and weather conditions. Time of cessation of activity was positively correlated to sunset time and maximum temperature, and negatively to windspeed. The duration of mid-day rest was not different among individuals, and positively correlated to maximum temperature. Most (86.6 %) of rests were at temperatures above 24 °C. Number of active fixes per day averaged 39.3 ± 5 S. D., with significant individual differences. For males mist depressed total active fixes, and daylength increased them, whereas for none of the females the environmental variables had any effect. Each day mongooses used on average 33.2 ± 16.8 % S. D. of their overall home ranges, without significant individual differences. The actual area used daily averaged 20.8 ± 21.5 ha S. D., with significant individual differences. Radio-tagged animals moved an average of 3,229 ± 1,135 m S. D. per day, with significant individual differences (Table). Males ranged daily over larger areas than females, and moved correspondingly more (Mann-Withney test, U = 430, $P < 0.01$, $n_1 = 20$, $n_2 = 31$). Movements were slower in the morning, increasing throughout the day, and faster in the afternoon (14.00 h to 17.00 h; Fig. 2). This increase corresponds to the peak in the "travelling" category in the time budget (Fig. 1). None of the three range use variables was significantly correlated with any environmental variable.

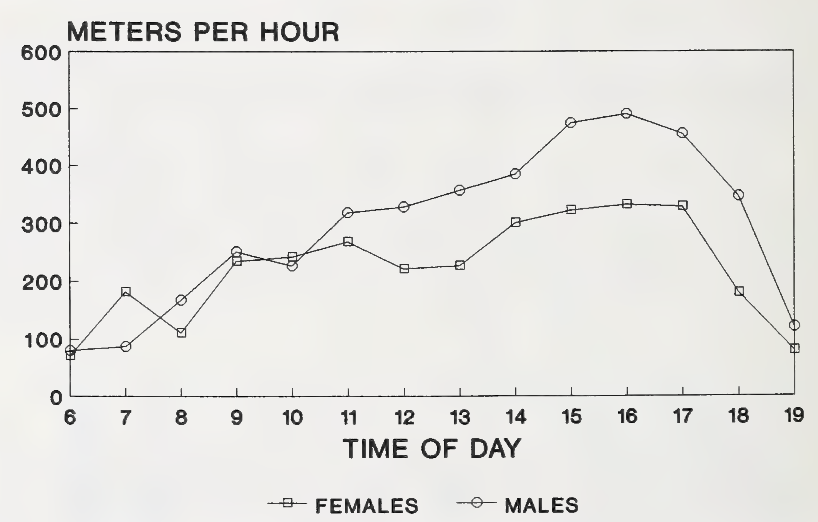


Fig. 2. Average movements of seven yellow mongooses *Cynictis penicillata* (4 females; 3 males) in the West Coast National Park in relation to time of day, during March–May 1991

Discussion

The environmental variables I investigated might have been associated with timing of activity, but not with the extent of movements, of yellow mongooses. The onset and end of activity, including the mid-day rest, may be related to weather through the availability of food resources. Indeed, both temperature and relative humidity have large influences on the foraging behaviour of termites (Nel et al. 1969), the main food source of *Cynictis* in this area (MacDonald and Nel 1986). Differences in meteorological conditions, including temperature, and sunrise times among different areas might therefore explain: (i) the discrepancy between the start of activity time (08.00 h–10.00 h) reported in Herzig-

Straschil (1977) and that (06.00 h–07.00 h) reported in Earlé (1981); (ii) the greater variability (07.15 h–12.00 h) found in the present study, which may be consistent with the greater variability in weather typical of a coastal region; (iii) the lack of consistency between the majority of studies of this species (e. g. Stuart 1981; Herzig-Straschil 1977), which indicate an exclusively diurnal activity, and two other authors (Earlé 1981; Smithers 1971), who suggest the occurrence of some nocturnal activity.

Acknowledgements

I wish to thank: the Trustees of the New Moorgate Trust Fund for the award of a John Ellerman Scholarship; Prof. J. A. J. Nel and Prof. R. Dallai for kindly providing facilities; the Oude Post Syndicate and the National Parks Board; D. Mostert, A. Craven, and especially N. L. Avenant for help both in the field and in the laboratory; F. Borsani for translating the German summary; Prof. S. Lovari, Prof. J. A. J. Nel, Dr. P. le FN. Mouton, and Dr. D. J. Holmes for comments on previous versions of this paper. This study was partly supported by Italian M.U.R.S.T.

Zusammenfassung

Aktivität der Fuchsmanguste Cynictis penicillata in einem Küstengebiet

Untersucht wurde die Tätigkeit der Fuchsmanguste *Cynictis penicillata* im Westküsten-Nationalpark (Cape Province, Südafrika). Der größte Teil der Individuen dieses Gebietes wurde gefangen und eine Stichprobe davon mit Radiohalsbändern versehen. Diese Tiere wurden mit Hilfe von Funkgeräten verfolgt. Tiere mit Halsbändern verhielten sich wie Tiere ohne Halsbänder. Die Mungos waren die meiste Zeit mit der Futtersuche beschäftigt. Anfang und Ende der Aktivitäten hingen von Sonnenauf- und -untergang sowie von der Lufttemperatur, der Windstärke und den Wetterbedingungen ab. Die Größe des täglichen Streifgebietes, dessen Verhältnis zum gesamten Aktionsraum sowie die tägliche Laufstrecke konnten mit keiner der genannten Variablen in Verbindung gebracht werden.

References

Boucher, C.; Jarman, M. L. (1977): The vegetation of the Langebaan area, South Africa. Trans. Royal Soc. South. Africa **42**, 241–288.

Cavallini, P. (1993): Spatial organization of the yellow mongoose *Cynictis penicillata*. Ethol. Ecol. and Evol. (in press.)

Cavallini, P.; Nel, J. A. J. (1990): Ranging behaviour of the Cape grey mongoose *Galerella pulverulenta* in a coastal area. J. Zool. (London) **222**, 353–362.

Earlé, R. A. (1981): Aspects of the social and feeding behaviour of the yellow mongoose *Cynictis penicillata* (G. Cuvier). Mammalia **45**, 143–152.

Hayne, D. W. (1949): Calculation of size of home range. J. Mammalogy **30**, 1–18.

Herzig-Straschil, B. (1977): Notes on the feeding habits of the yellow mongoose *Cynictis penicillata*. Zool. Afr. **12**, 225–229.

MacDonald, J. T.; Nel, J. A. J. (1986): Comparative diets of sympatric small carnivores. South African J. Wildl. Res. **16**, 115–121.

Nel, J. J. C.; Hewitt, P. H.; Smith, L. J.; Smit, W. T. (1969): The behaviour of the harvester termite (*Hodotermes mossambicus* (Hagen)) in a laboratory colony. J. entom. Soc. South. Africa **32**, 9–24.

Rice, W. R. (1989): Analyzing tables of statistical tests. Evolution **43**, 223–225.

Siegel, S. (1956): Nonparametric statistic for the behavioural sciences. New York: McGraw-Hill.

Skinner, J. D.; Smithers, R. H. N. (1990): The mammals of the southern African subregion. Sec. ed. Pretoria, South Africa: University of Pretoria.

Smithers, R. H. N. (1971): The mammals of Botswana. Mem. Nat. Mus. Rhod. **4**, 1–230.

Stuart, C. T. (1981): Notes on the mammalian carnivores of the Cape Province, South Africa. Bontebok **1**, 1–58.

Swihart, R. K.; Slade, N. A. (1985): Influence of sampling interval on estimates of home-range size. J. Wildl. Manage. **49**, 1019–1025.

Author's address: Dr. Paolo Cavallini, Department of Evolutionary Biology, Università di Siena, via Mattioli 4, I-53100 Siena, Italy

Z. Säugetierkunde 58 (1993) 286–293

ISSN 0044-3468

The diet of Risso's dolphin, *Grampus griseus* (Cuvier, 1812), from the east coast of South Africa

By V. G. Cockcroft, Sharon L. Haschick, and N. T. W. Klages

Centre for Dolphin Studies, Port Elizabeth Museum, Humewood, South Africa

Receipt of Ms. 7. 10. 1992
Acceptance of Ms. 2. 3. 1993

Abstract

Examined the stomach contents of Risso's dolphins (*Grampus griseus*), stranded along the east coast of South Africa over a 22 year period (1969–1991). Prey consisted exclusively of cephalopods from which seventeen species were identified. Index of relative importance values were used to identify the most important prey. The most dominant prey *Loligo vulgaris reynaudii*, a shallow water, semi-pelagic subspecies constituted 81 % by mass of the total prey and 48.1 % and 29.2 % by number and frequency of occurrence, respectively. Other important species, were *Lycoteuthis diadema, Argonauta nodosa, Octopus magnificus* and *Ancistrocheirus lesueuri*. The diversity of prey species differed for males and females and also between dolphin size classes. These data suggest a partitioning of food resources between sub-groups. The results of this study indicate that Risso's dolphins probably feed in the Agulhas current and also in coastal waters where the continental shelf is narrow.

Introduction

The diets of cetaceans are determined to a large extent by their geographical location, as well as the seasonal and topographical changes in the abundance of their prey (Clarke 1986a). Risso's dolphins, *Grampus griseus*, are widespread in warm tropical and temperate pelagic (> 1000 m) waters (Aguayo 1975; Jennings 1982; Ross 1984). They are also frequently sighted at the continental shelf edge (Leatherwood et al. 1982; Ross 1984) and in coastal waters where the shelf is narrow.

Risso's dolphins feed almost exclusively on cephalopods (Tomilin 1957; Tsutsumi et al. 1961; Orr 1966; Stroud 1968; Mitchell 1975; Leatherwood et al. 1982; Ross 1984; Clarke and Pascoe 1985; Sekiguchi et al. 1992). Though the specific or generic identity of the prey species and their relative importance in the diet is not generally known. A knowledge of the prey preferences and the relationship of the diet to the social structure and movements of Risso's dolphins provides a better understanding of their biology.

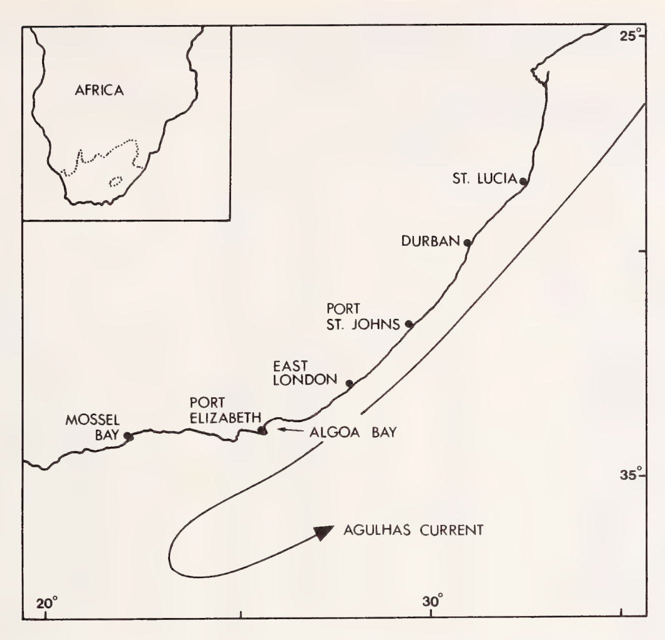
The aim of this study was to assess quantitatively the diet of Risso's dolphins stranded on the east coast of southern Africa, between Mossel Bay (34 °S, 22 °E), and St Lucia, Natal (28° 30′ S, 32° 30′ E) (Figure).

Material and methods

This study examined the stomach contents of 65 Risso's dolphins stranded between 1969 and 1991, and includes a re-examination of seven stomachs reported by Ross (1984). Stomachs were excised and washed in water until all loose tissue was removed and sorted (sensu Cockcroft and Ross 1990). Loose cephalopod beaks were stored in 10 % buffered formalin for later identification. Data recorded from strandings included date and locality of stranding, length and mass and sex of individuals.

Identification of prey remains used the Port Elizabeth Museum's reference collection of some 1,600 beaks of almost 300 cephalopod species. For each species, regressions relating beak dimension to prey weight and length are available. Cephalopod classification follows that of Clarke (1986b).

Beaks of all cephalopod species, except octopods and sepiids, were measured across the lower rostral length (LRL), to the nearest 0.05 mm, using Vernier calipers. The hood length (HL) was



The south-east coast of South Africa (see text for definition). The Agulhas current is a major oceanographic feature of the area and its flow follows the continental shelf edge

measured in the case of octopods and sepiids. Mantle length and reconstituted prey mass were then calculated from the beak measurements, using the appropriate regressions from the reference collection.

The minimum number of individuals of any cephalopod species in a stomach was assumed to be the greater number of either upper or lower beaks. Where upper beak numbers were larger, the length and mass of prey were determined from estimated lower beak dimensions.

The reconstituted mass of prey species within stomachs was determined from the established regressions. Where regressions were not available, reconstituted mass and length were extrapolated from available records. An index of relative importance (IRI) was calculated for each species according to Pinkas et al. (1971), where: IRI = (% number + % reconstituted mass) × % frequency of occurrence.

Results

Thirty three of the 65 stomachs were completely empty and the remaining 32 contained only cephalopod remains, though statistical analyses were based on all stomachs. From a total of 1341 prey items, 17 distinct species were identified; ten to known specific level and seven to unidentified species within known genera (Tab. 1).

Based on calculated Index of Relative Importance (IRI) values, the five most important prey species in the diet were; *Loligo vulgaris reynaudii, Lycoteuthis diadema, Argonauta nodosa, Octopus magnificus* and *Ancistrocheirus lesueri* (Tab. 1). These species were also the five most important by reconstituted mass and together contributed almost 92 % of the total reconstituted mass of prey taken (Tab. 1). However, *L. v. reynaudii* and *L. diadema* were clearly the most important in terms of frequency of occurrence and total numbers (Tab. 1).

Although there were similarities in the prey consumed by males and females, there was a significant difference (Diversity Index Comparison, t-test: t = 10.8, df = 1303, $P < 0.05$) in the diversity of prey they consumed (Tab. 2). Four species consumed by females were not found in males (Tab. 2).

Table 1. **Prey of Risso's Dolphins off the south-east coast of South Africa and their contribution to the diet**

Based on their absolute number, frequency of occurrence *(f)*, *reconstituted* mass (recon. mass), mean prey length, percentage number, percentage mass, percentage frequency of occurrence and Index of Relative Importance (iri)

Species	No.	*f*	recon. mass (g)	mean length (mm)	% No.	% mass	% *f*	iri
Order Sepiida								
Sepia sp.	21	3	70	40	1.6	0.0	4.6	7
Order Teuthida								
Loligo v. reynaudii	644	19	272458	262	48.0	81.0	29.2	3770
Lycoteuthis diadema	390	16	16430	96	29.1	4.9	24.6	836
Ancistrocheirus lesueuri	16	7	7512	188	1.2	2.2	10.8	37
Octopoteuthis sp.	14	6	3134	162	1.0	0.9	9.2	18
Moroteuthis sp.	4	3	231	5	0.3	0.1	4.6	2
Histioteuthis sp.	2	2	995	150	0.1	0.3	3.1	1
Brachioteuthis sp.	34	4	215	67	2.5	0.1	6.2	16
Todarodes angolensis	14	2	4574	230	1.0	1.4	3.1	7
Chiroteuthis veranyi	26	7	987	110	1.9	0.3	10.8	24
Teuthowenia pellucida	22	4	1739	202	1.6	0.5	6.2	13
Megalocranchia sp.	6	1	714	323	0.4	0.2	1.5	1
Cranchia scabra	32	6	1383	115	2.4	0.4	9.2	26
Order Vampyromorpha								
Vampyroteuthis infernalis	9	4	461	48	0.7	0.1	6.2	5
Order Octopoda								
Opisthoteuthis sp.*	8	3	337	56	0.6	0.1	4.6	3
Octopus magnificus	19	6	16081	160	1.4	4.8	9.2	57
Argonauta nodosa	80	8	9223	81	6.0	2.7	12.3	107
Total	1341		336550	135				

* No regressions available, length and mass estimated.

The largest cephalopod consumed was estimated at almost 400 mm (*O. magnificus*) and the smallest at 5 mm (*Sepia* sp.), although the calculated lengths of most prey fell between 100 and 200 mm, with a mean of approximately 140 mm (Tab. 1). However, the mean length of the dominant prey item (*L. v. reynaudii*) was greater and estimated at 262 mm (Tab. 1).

There was a poor correlation between dolphin length and both mean length of prey taken ($r = 0.26$) and the total reconstituted mass of prey consumed ($r = 0.28$). Generally, however, the maximum length of prey consumed increased with dolphin length and small cephalopod species (e.g. *Sepia* sp., mean length = 56 mm), which were important in the diet of smaller dolphins, were not taken by larger dolphins (Tab. 3). Similarly, larger cephalopod species, such as *Todarodes angolensis* (mean length = 230 mm) and *O. magnificus* (mean length = 160 mm) were important for larger dolphins, but were not taken by smaller dolphins. The mean length of the prey of males (208 mm) was significantly greater than that of females (146 mm) (Student's t-test: $t = 12.79$, $df = 1336$, $P < 0.05$). In contrast, there was no significant difference between the total mass of prey taken by individual males and females (Student's t-test: $t = 0.95$, $df = 30$, $P > 0.05$).

There was no significant difference between the diversity of prey items taken by large (> 250 cm) and small dolphins (< 250 cm) (Diversity Index Comparison, t-test: $t = -1.81$, $df = 881$, $P > 0.05$). Likewise, there was no significant difference between the mean length of prey taken by these two classes (Student's t-test: $t = 0.326$, $df = 24$, $P > 0.05$).

Table 2. **Index of Relative Importance (iri) and rank of importance of the prey taken by male and female Risso's dolphins**

Species	Males		Females	
	iri	rank	iri	rank
Order Sepiida				
Sepia sp.	1		20	
Order Teuthida				
Loligo v. reynaudii	4987	1	2633	1
Lycoteuthis diadema	687	2	1048	2
Ancistrocheirus lesueuri	32	6	55	7
Octopoteuthis sp.	4	9	52	8
Moroteuthis sp.	4	10	1	
Histioteuthis sp.			7	
Brachioteuthis sp.			67	6
Todarodes angolensis			38	10
Chiroteuthis veranyi	11	7	50	9
Teuthowenia pellucida	41	4	3	
Megalocranchia sp.			5	
Cranchia scabra	1		93	5
Order Vampyromorpha				
Vampyroteuthis infernalis	1		15	
Order Octopoda				
Opisthoteuthis sp.*	5	8	2	
Octopus magnificus	33	5	125	3
Argonauta nodosa	145	3	101	4
Number of stomachs	25		34	

* No regressions available, length and mass estimated.

The mean number of prey per stomach was 42 (range 1–282). There was little correlation ($r = 0.018$) between the mean number of prey per stomach and dolphin length. Additionally, there was no significant difference between the number of prey taken by males and females (Anova: $F = 0.255$, $df = 30$, $P > 0.05$).

In general, the prey variety in any stomach was low (mean of 3 species, range 1–9), with little correlation between the length of dolphin and the number of prey species taken ($r = 0.063$). Also, there was no significant difference between the number of prey species consumed by males and females (Anova: $F = 1.599$, $df = 30$, $P > 0.05$).

A total of nine stomachs were examined from animals stranded in summer (October–March) and 25 from those stranded in winter (April–September). Despite these low numbers, there was a significant difference between the diversity of prey species taken in winter and summer (Diversity Index Comparison, t-test: $t = 18.83$, $df = 1204$, $P < 0.05$), with eight species taken in winter not consumed in summer (Tab. 4).

Discussion

The interpretation of cetacean diet based on analyses of the stomach contents of stranded individuals may be subject to a number of biases (Ross 1984; Clarke 1986a; Sekiguchi et al. 1992). Firstly, the apparent ill health of the majority of singly stranded cetaceans (Ross 1984) may result in either an empty stomach, or the stomach containing only a few typical prey items eaten prior to the illness. Secondly, the dietary importance of cephalopods is easily overestimated, because their hard remains (beaks) are retained and are identifiable

Table 3. **Index of Relative Importance (iri) values, rank of importance and mean length of the prey taken by large (>250 cm) and small (<250 cm) Risso's dolphins**

Species	Dolphin length >250 cm			Dolphin length <250 cm		
	iri	rank	mean length (mm)	iri	rank	mean length (mm)
Order Sepiida						
Sepia sp.				167	6	56
Order Teuthida						
Loligo v. reynaudii	8215	1	262	3030	2	255
Lycoteuthis diadema	543	2	99	7243	1	98
Ancistrocheirus lesueuri	47	5	173	257	4	208
Octopoteuthis sp.	12	11	174		5	147
Moroteuthis sp.	6	13	5	20		
Histioteuthis sp.	1	15	137	137	11	162
Brachioteuthis sp.	8	12	65		8	77
Todarodes angolensis	26	7	230	144		
Chiroteuthis veranyi	25	8	119	28	7	103
Teuthowenia pellucida	28	6	204	37		196
Megalocranchia sp.				275	9	323
Cranchia scabra	12	10	120		3	114
Order Vampyromorpha						
Vampyroteuthis infernalis	19	9	48			
Order Octopoda						
Opisthoteuthis sp.*	6	14	82	8	12	42
Octopus magnificus	192	4	160			
Argonauta nodosa	286	3	81	36	10	79
Number of stomachs		24			9	

* No regressions available, length and mass estimated.

for longer periods than fish otoliths (Clarke and MacLeod 1982; Bigg and Perez 1985; Clarke 1986a). For pelagic animals, both these sources of bias may be compounded by the remains of prey consumed during the animal's transit of inshore waters before beaching (Ross 1984; Clarke 1986a).

At least two studies have attempted to quantify any biases inherent in dietary studies from stranded cetaceans. In a comparison of the diet of non-stranded and stranded animals, Sekiguchi et al. (1992) demonstrated that the latter were biased, but a similar analysis by Ross (1984) showed no such bias. In view of the contradictory nature of these two studies, interpretations from the present study are assumed to reflect the diet of Risso's dolphins from the east coast of South Africa.

Like the study of Ross (1984), this study indicates that Risso's dolphins off the south-east coast of South Africa feed exclusively on cephalopods. Although Risso's dolphins consume at least 17 species, their diet is dominated by the 'chokker' squid, *L. v. reynaudii*, a fairly common cephalopod inhabiting the south-east coast of South Africa (Augustyn 1990). Based on calculated IRI values and reconstituted weights of stomach contents, four other cephalopods were also important in the diet (*A. lesueuri, A. nodosa, L. diadema,* and *O. magnificus*). Though there was some small variation in the relative importance of these five major prey, their continued presence throughout the study and for all size and sex classes of dolphins, is significant and may reflect their relative availability in this region.

Exclusive cephalopod diets are also recorded for Risso's dolphins stranded or captured in British waters (Tomlin 1957), the Mediterranean (Pilleri and Gihr 1969), Japanese waters (Tsutsumi et al. 1961) and the eastern Pacific (Orr 1966; Stroud 1968). Addition-

Table 4. **The relative importance (percentage mass, number and frequency) (*f*) of occurrence and Index of Relative Importance (iri) of the prey of Risso's dolphins taken in winter (April–September) and summer (October–March)**

Species	Winter				Summer			
	% mass	% No.	% *f*	iri	% mass	% No.	% *f*	iri
Order Sepiida								
Sepia sp.	0.1	2.6	6.8	18				
Order Teuthida								
Loligo v. reynaudii	60.0	21.9	31.8	2606	89.3	31.6	93.4	5570
Lycoteuthis diadema	12.8	46.8	34.1	2032	0.9	5.3	0.0	5
Ancistrocheirus lesueuri	2.8	1.3	11.4	47	0.9	10.5	1.8	29
Octopoteuthis sp.	2.3	1.5	11.4	43	0.4	5.3	0.1	2
Moroteuthis sp.	0.2	0.5	6.8	5				
Histioteuthis sp.	0.8	0.2	4.5	5				
Brachioteuthis sp.	0.2	4.1	9.1	39				
Todarodes angolensis	3.6	1.7	4.5	24				
Chiroteuthis veranyi	0.8	3.0	13.6	52	0.2	5.3	0.0	1
Teuthowenia pellucida	1.0	1.9	9.1	27	1.1	5.3	0.2	7
Megalocranchia sp.	0.6	0.7	2.3	3				
Cranchia scabra	1.1	3.9	13.6	68				
Order Vampyromorpha								
Vampyroteuthis infernalis	0.4	1.1	9.1	13	0.2	5.3	0.0	1
Order Octopoda								
Opisthoteuthis sp.*	0.3	1.0	6.8	8				
Octopus magnificus	8.1	0.7	6.8	60	2.6	21.1	3.2	124
Argonauta nodosa	5.2	6.9	15.9	193	4.3	5.3	1.2	29
Number of stomachs				44				19

* No regressions available, length and mass estimated.

ally, Risso's dolphins in captivity accept only squid (Tsutsumi et al. 1961). Other than two fish species found in the stomachs of Risso's dolphins stranded off South Africa (Sekiguchi et al. 1992), no fish remains have been found in this species. These data infer that Risso's dolphins consume a small variety of locally abundant cephalopod prey and that it is inappropriate to consider this species an opportunistic predator. This is not unusual, some cetaceans are relatively restricted in their diet, regularly feeding on only a few types of prey (Fiscus 1982).

Though most of the cephalopod prey taken by Risso's dolphins are oceanic, benthic neritic and mid-water neritic species are also consumed (Roper et al. 1984; Clarke 1986a; Clarke 1986b). These data indicate that Risso's dolphins feed not only in the epi- and meso-pelagic zones of the ocean, but also over the continental slope and shelf areas. However, the dominant prey species (*L. v. reynaudii*) is neritic, inferring that Risso's dolphins feed primarily over the continental shelf. Although this conclusion may be influenced by the biases discussed earlier, Risso's dolphins are sighted most frequently along the continental shelf edge and are often seen in coastal waters where the shelf is narrow (Leatherwood et al. 1982; Ross 1984). Additionally, Risso's dolphin distribution is probably related to the movements of their prey, as is that of other pelagic dolphins (Norris and Dohl 1980). In combination, these data suggest that the present results reflect the normal diet of Risso's dolphins for the south-east coast of South Africa.

Most of the cephalopod species eaten by Risso's dolphins are ammoniacal, buoyant, solitary species, evenly and widely distributed, while the remainder are muscular, fast

swimmers, occurring in large aggregations (CLARKE 1986a). Dolphins which occur in small groups, like Risso's dolphins, are known to prey on species with the former characteristics (ROSS 1984) and this may explain the great variety of ammoniacal squid eaten. The latter characteristics are typical of *L. v. reynaudii* and almost certainly account for this species' high frequency of occurrence and abundance in individual stomachs. It is interesting that 70 % of all Risso's dolphin prey, both oceanic and neritic, are luminous or have photophores (CLARKE 1986a), possibly making their capture easier.

Male and female Risso's dolphins take different prey sizes and although there was no clear relationship between dolphin and prey size, larger dolphins consumed larger cephalopod prey than smaller dolphins. Though the latter may only be a result of the physical limitations of the smaller mouths of small dolphins, these data in combination, indicate some form of sex, and perhaps size, related partitioning of available resources. Risso's dolphins generally occur in small groups that are often part of a larger, widespread aggregation (ROSS 1984). Although the size and sex structure of these groups is unknown, it seems feasible that they may be sex or size based to alleviate competition for resources. Such sex and size group partitioning is evident in bottlenose, and perhaps other dolphins, where sub-groups exploit different foraging ranges, prey sizes and species, to reduce intraspecific competition (COCKCROFT and ROSS 1990).

The reasons for the seasonal variation in the prey spectra of Risso's dolphins is unknown. Although this may be an artifact of the differing seasonal frequency of strandings, it may also reflect seasonal changes in the availability of the prey, especially the summer abundance of *L. v. reynaudii* (ROPER et al. 1984).

The fishery for *L. v. reynaudii* is the most important commercial fishery off the south-east coast of South Africa (AUGUSTYN 1990) and it is expanding rapidly. This cephalopod is also an important and primary food resource for Risso's dolphins and other marine mammals (ROSS 1984; CASTLEY et al. 1991; YOUNG 1993) off the south-east coast of South Africa. In view of the current level and envisioned expansion of the commercial fishery, there may be existing and potential competition for this resource between fisheries and marine mammals. Consequently, an assessment of the impact of marine mammals on cephalopod stocks and the determination of the extent and potential interactions between fisheries and marine mammals is important.

Acknowledgements

We would like to thank the Foundation for Research Development, University of Port Elizabeth and Port Elizabeth Museum for financial assistance.

Zusammenfassung

Die Nahrung von Risso's Delphinen, Grampus griseus (Cuvier, 1812) an der südafrikanischen Ostküste

Untersucht wurden die Mageninhalte von 65 gestrandeten Risso's Delphinen (*Grampus griseus*), die über einen Zeitraum von 22 Jahren (1969–1991) an der südafrikanischen Ostküste gesammelt worden waren. Ausschließlich Tintenfische, insgesamt 17 verschiedene Taxa, wurden anhand ihrer unverdaulichen Schnäbel als Beute identifiziert. *Loligo vulgaris reynaudii*, ein semi-pelagischer Tintenfisch aus dem Flachwasser des Kontinentalschelfes, dominierte die Nahrung mit 81 % Gewichtsanteil, machte 48.1 % aller gezählten Cephalopoden aus und erschien in 29.2 % aller Mägen mit Inhalt. *Lycoteuthis diadema, Argonauta nodosa, Octopus magnificus* und *Ancistrocheirus lesueuri*, sämtlich Arten, die am Schelfabhang vorkommen, waren die nächst wichtigsten Nahrungstiere. Die Artenzusammensetzung der Beute deutet daraufhin, daß Risso's Delphine ihre Nahrung im warmen Agulhas Strom über dem Schelfabhang finden, aber auch dort in Küstengewässern, wo der Kontinentalschelf schmal ist. Geschlechts- und größenspezifische Unterschiede in der Beutewahl wurden ermittelt. Diese Daten lassen vermuten, daß eine Aufteilung von Nahrungsresourcen zwischen sozialen Gruppen stattfindet.

References

AGUAYO, L. A. (1975): Progress report on small cetacean research in Chile. J. Fish. Res. Board Can. **32**, 925–926.

AUGUSTYN, C. J. (1990): Biological studies on the Chokker squid *Loligo vulgaris reynaudii* (Cephalopoda; Myopsida) on spawning grounds off the south-east coast of South Africa. S. Afr. J. Sci. **9**, 11–26.

BIGG, M. A.; PEREZ, M. A. (1985): Modified volume: A frequency volume method to assess marine mammal food habits. In: Marine Mammals and Fisheries. Ed. by J. R. BEDDINGTON, R. H. BEVERTON, and D. M. LAVIGNE. London: George Allen and Unwin. Pp. 277–283.

CASTLEY, J. G.; COCKCROFT, V. G.; KERLEY, G. I. H. (1991): A note on the stomach contents of fur seals *Arctocephalus pusillus pusillus* beached on the south east coast, South Africa. S. Afr. J. mar. Sci. **11**, 573–577.

CLARKE, M. R. (1986a): Cephalopods in the diet of Odontocetes. In: Research on Dolphins. Ed. by E. E. BRYDEN and R. HARRISON. Oxford: Clarendon Press. Pp. 281–321.

— (1986b): A handbook for the identification of cephalopod beaks. Oxford: Clarendon Press.

CLARKE, M. R.; MACLEOD, N. (1982): Cephalopods in the diet of Elephant seals at Signey Island, South Orkney Islands. Br. Antarct. Bull. **57**, 27–31.

CLARKE, M. R.; PASCOE, P. L. (1985): The stomach contents of a Risso's Dolphin (*Grampus griseus*) stranded at Thurleston, South Devon. J. mar. biol. Ass. U.K. **65**, 663–665.

COCKCROFT, V.; ROSS, G. J. B. (1990): Food and feeding of the Indian Ocean bottlenose dolphin. In: The Bottlenose Dolphin. Ed. by S. LEATHERWOOD and R. R. REEVES. New York: Academic Press. Pp. 295–308.

FISCUS, C. H. (1982): Predation by marine mammals on squids of the Eastern North Pacific Ocean and the Bering Sea. Mar. Fish. Rev. **44**, 1–10.

JENNINGS, R. (1982): Pelagic sightings of Risso's dolphin, *Grampus griseus*, in the Gulf of Mexico and Atlantic Ocean adjacent to Florida. J. Mammalogy **63**, 522–523.

LEATHERWOOD, S.; PERRIN, W. F.; EVANS, W. E. (1982): Whales, dolphins and porpoises of the eastern North Pacific and adjacent Arctic waters. A guide to their identification. NOAA Tech. Rep. NMFS. Circ. **444**, 129–133.

MITCHELL, E. D. (1975): Report on the meeting on smaller cetaceans. Montreal, April 1–11, 1974. In: Review of biology and fisheries for smaller cetaceans. J. Fish. Res. Board Can. **32**, 925–927.

NORRIS, K. S.; DOHL, T. P. (1980): The structure and function of cetacean schools. In: Cetacean Behaviour: Mechanisms and Functions. Ed. by L. M. HERMAN. New York: Wiley and Sons. Pp. 211–262.

ORR, R. T. (1966): Risso's dolphins on the Pacific coast of North America. J. Mammalogy **47**, 341–343.

PILLERI, G.; GIHR, M. (1969): On the anatomy and behaviour of Risso's dolphin (*Grampus griseus* G. Cuvier). Invest. Cetacea. **1**, 74–93.

PINKAS, L.; OLIPHANT, M. S.; IVERSON, I. L. K. (1971): Food habits of albacore, bluefin tuna and bonito in California waters. Calif. Dept. Fish Game, Fish Bull. **152**, 105–109.

ROPER, C. F. E.; SWEENY, M. J.; NAUEN, C. E. (1984): FAO species catalogue: Vol. 3. Cephalopods of the World. An annotated and illustrated catalogue of species of interest to fisheries. FAO Fish. Synop., (125) Vol. **3**.

ROSS, G. J. B. (1984): The smaller cetaceans of the south-east coast of southern Africa. Ann. Cape Prov. Mus. (nat. Hist.) **11**, 259–327.

SEKIGUCHI, K.; KLAGES, N.; BEST, P. (1992): A review of diets of smaller odontocete cetaceans along the Southern African Coast. S. Afr. J. mar. Sci. **12**, 843–861.

STROUD, R. K. (1968): Risso's dolphin in Washington State. J. Mammalogy **49**, 347–348.

TOMILIN, A. G. (1957): Mammals of the U.S.S.R. and adjacent countries. Vol. IX. Cetacea. Jerusalem: Israel Program for Scientific Translations 1967.

TSUTSUMI, T.; KAMIMURA, Z.; MIZUE, K. (1961): Studies on the little toothed whales in the West Sea Areas of Kyusyu-V. About the food of the little toothed whales. Bull. Fac. Nagasaki Univ. **11**, 19–28.

YOUNG, D. D. (1993): Diet in free-ranging and stranded common dolphins (*Delphinus delphis*, Linnaeus), from the south-east coast of southern Africa. Unpubl. M. Sc. thesis, Univ. of Port Elizabeth, South Africa.

Authors' addresses: VICTOR G. COCKCROFT and NORBERT T. W. KLAGES, Centre for Dolphin Studies, Port Elizabeth Museum, P.O. Box 13147, Humewood, 6013, South Africa; SHARON L. HASCHICK, Department of Zoology, University of Port Elizabeth, P.O. Box 1600, Port Elizabeth, 6000, South Africa

Z. Säugetierkunde 58 (1993) 294–301

ISSN 0044-3468

Social grouping dynamics of Mouflon *(Ovis ammon)* during rut

By R. Bon, J. Badia, Marie L. Maublanc, and J. M. Recarte

Institut de Recherches sur les Grands Mammifères, Institut National de la Recherche Agronomique, Castanet Tolosan, France

Receipt of Ms. 10. 6. 1992
Acceptance of Ms. 1. 4. 1993

Abstract

Studied grouping dynamics of mouflons in relation to the presence of males during rut in October-December. Before rut, older males and females were strongly segregated. During rut, the monthly group size distributions closely fit truncated negative binomial distributions. In October, mouflons lived in small groups and males entered female ranges. Single adult rams, especially older ones, wandered looking for œstrous ewes while younger rams were mostly in matriarchal groups in forested areas. In October, the observed sex ratio was male-biased. In November, mouflons used more open areas, the sex ratio declined and group size increased. The male population observed included few older rams per potentially receptive female. We suggest that the rut delayed the aggregative tendency and resulted in high social instability. Adult males provoked dissociation of mother-lamb bonds during the mating peak. Male lambs appeared more disturbed than female lambs but returned earlier in ewe groups. In December, males over 6 years old were rarely observed with females, whereas younger rams stayed with ewes up to January, when mouflons frequently formed large groups.

Introduction

Despite the great interest of ethologists and ecologists in the social behaviour and mating systems of ungulates, very little is known about the social organization of the mouflon *(Ovis ammon)*. This dimorphic gregarious species exhibits a high degree of sexual segregation outside the rut (Pfeffer 1967; Gonzalez 1985; Bon and Campan 1989) like other wild sheep (Geist 1971) and feral sheep (Grubb and Jewell 1966). In Europe, the rut occurs from the end of October to the end of December (see Pfeffer 1967 for a review).

Wild sheep have a promiscuous mating system. Rams neither hold harems nor defend territories (Pfeffer 1967; Geist 1971; Hogg 1984, 1987), but wander in search of receptive females. The gathering of males and females entails large social modifications in open-membership groups (Bon and Campan 1989).

The aim of this study was to investigate when rams associate with ewes according to their age. To what extent social and ecological factors may account for the changes of composition and size of groups during rut is discussed.

Material and methods

Study area

The study area is situated in the Caroux-Espinouse massif (42.5° N, 3° E, elevation 300 to 1100 m) in France. After a summer dryness, cooler temperatures and rainfall allow a new growth of grasses. In winter, food availability decreases as reflected by mouflon rumen contents (Bon et al. 1990).

The study population is protected in the hunting reserve (1830 ha) and is hunted elsewhere from September to February (Cugnasse 1982). Between 1977 and 1989, 1437 males and 1403 females were hunted but the mean age of rams shot was higher than that of females (male range: 5–6.6 years, female range: 3.1–4.5 years). No natural large predators are present.

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5805-0294 $ 02.50/0

Data collection

From July to January in 1984, 1985 and 1986, group sizes and composition were noted during 53 ground surveys along hiking routes, early in both morning and afternoon during the maximum feeding periods of mouflons. In 1984 and 1985, we walked along two routes in the hunting reserve. Throughout 1986, the sampled area was enlarged by eight new routes, covering about one half of the 10,000 ha used by the mouflon population. A group was defined as a set of animals within 25 m of one another. During the walks, 6460 observations of mouflons were collected, and ascribed to the following age/sex classes: male and female lambs (M1 and F1 respectively), females ≥ 1 year old (F), yearling males (M2), 2-year-old males (M3), 3 to 6-year-old males (M4), males ≥ 7 years old (M5). Groups were classified as adult or yearling male alone (M), adult and yearling male groups (MM), matriarchal groups, mixed sex groups were with or without lambs.

In the Caroux-Espinouse, the rut extends from October to early January with the peak of œstrus occurring in the first half of November (Bon et al. 1992). All ewes ≥ 1.5 years old were considered as potentially receptive during autumn (Cugnasse et al. 1985; Bon et al. 1993). The sex ratio of the breeding population (M/F) was measured including all mouflons ≥ 1.5 years.

Statistical analysis

The proportion of age/sex class, the group size and composition and the social tendencies of animals of each age/sex class were analysed monthly. Summer results are presented to underline social changes during rut.

Age/sex class proportion

Because few animals were marked and because the population was sampled repeatedly, our data are probably not independent and the age/sex proportions were only represented graphically. Because lamb sex could not be determined, lambs of both sexes were pooled in summer.

Group size

Adult males joined females in October, so we only studied the effect of male presence on group size from October. In order to study the monthly grouping tendency during rut, we looked for the probability distribution of the random variable "group size" (noted Y).

Number of groups and group sizes might partially account for the observed group size distribution patterns. In order for these two variables to explain the variance in the data, we had to design a model in which each variable was represented by an appropriate theoretical distribution. The resulting mixed distribution was compared to the distribution of the mouflon data. We assumed that the number of mouflons in a group is given by a simple Poisson process with mean λ, where λ varies according to a gamma distribution from group to group.

Denote by y an observed value of Y, the probability function for the Poisson distribution is:

$$\lambda^y \frac{e^{-\lambda}}{y!} \tag{1}$$

where λ is an independently distributed gamma variable with a probability density function given by:

$$\left[p^k \Gamma(k)\right]^{-1} \lambda^{k-1} e^{-\frac{\lambda}{p}}; \lambda > 0; k > 0; p > 0 \tag{2}$$

where p is the scale parameter and k the shape parameter (if $0 < k < 1$ the density has a pole at the origin and decreases monotonously as $\lambda \to \infty$; if $k > 1$ the density is zero at the origin and has a single mode. The graphs of the densities are all positively skewed).

Making these two assumptions, we determined the probability function of Y when heterogeneous groups are mixed. With the joint distribution of y and λ obtained from the product of (1) and (2), we integrated over λ (from zero to infinity) to express the probability function of Y. For the compounding of a gamma with a Poisson distribution, this yields a negative binomial probability function (Johnson and Kotz 1969).

$$P[Y = y] = [p^k \Gamma(k)]^{-1} \int_0^{\infty} \lambda^{k-1} e^{-\frac{\lambda}{p}} (\lambda^y \frac{e^{-\lambda}}{y!})\, d\lambda$$

$$P[Y = y] = \left(\frac{y + k - 1}{y}\right) \frac{p^y}{(1 + p)^{k+y}}$$

The distribution of Y must be described by a truncated negative binomial distribution because groups of size 0 cannot be observed. The truncated negative binomial probability function is given by:

$$P[Y = y] = \binom{y + k - 1}{y} \frac{p^y}{(1 + p)^y[(1 + p)^k - 1]}$$

with expectation,

$$E(Y) = \frac{kp(1 + p)^k}{(1 + p)^k - 1} \quad (3)$$

and variance,

$$V(Y) = E(Y)\,[1 + p + kp - E(Y)] \quad (4)$$

We estimated the parameters k and p of the model by the maximum likelihood method.

With respect to the truncated Poisson distribution, the truncated negative binomial distribution becomes increasingly overdispersed as the value of the p parameter rises. At the limit, when $p \to 0$, $k \to \infty$ and $kp \to$ the mean, the truncated negative binomial distribution tends towards a truncated Poisson distribution ((4) $\Longrightarrow$ V(Y) = E(Y)). Thus, k and p (or E(Y) and V(Y)) can be viewed as aggregation indices because a p value which is not too small and a small k value (or V(Y) > E(Y)) indicate a non-random distribution of mouflons in the study area.

In order to assess the goodness of fit of the model to the data, we used a χ^2 test with degrees of freedom equal to the number of observed frequencies minus three because there are two parameters k and p and the sum of the predicted values must be equal to the total number of groups observed.

Results

Age/sex class proportions

In summer, rams $\geq$ 3 years old lived in more closed habitats than ewes (n = 452) so the observed ratios were strongly biased towards ewes (M/F = 0.29, M2/F = 0.13, M3/F = 0.035, M4/F = 0.13, M5/F = 0).

In October, we saw more males than females (M/F = 1.29) and the ratio of each male class to females (n = 157) peaked (M2/F = 0.22, M3/F = 0.14, M4/F = 0.8, M5/F = 0.13). From November to January, the yearling males/females ratio was similar to that seen in summer (respectively 0.13, 0.08 and 0.13) while the proportion of rams $\geq$ 2 years old decreased at a rate which rose with ram age. In November, when most conceptions occurred, for every 100 ewes (n = 930) we recorded 3 males $\geq$ 7 years old, 29 males 3 to 6 years old and 9 males 2 years old. In December, males $\geq$ 7 years old were rarely observed (M5/F = 0.007) whereas younger ones (M4/F = 0.2, M3/F = 0.08) stayed in the female (n = 772) ranges. As the rut progressed, adult ewes became more and more numerous in the samples (in January M5/F = 0.002, M4/F = 0.15, M3/F = 0.006 for n = 1235 females).

The proportion of lambs decreased from October (M1/F = 0.25, F1/F = 0.35) to November (M1/F = 0.14, F1/F = 0.22) and recovered in December (M1/F = 0.20, F1/F = 0.19) and January (M1/F = 0.20, F1/F = 0.27). In order to assess the possible effects of the presence of rams, the lambs/ewes ratio for both sexes were measured in mixed and matriarchal groups. The ratios were systematically higher in matriarchal than in mixed groups for both sexes, although the differences were not significant in October (F1/F = 0.42 vs F1/F = 0.36, G = 0.16, P = 0.69; M1/F = 0.35 vs M1/F = 0.25, G = 0.76. P = 0.38), December (F1/F = 0.20 vs F1/F = 0.19, G = 0.04, P = 0.85; M1/F = 0.23 vs M1/F = 0.195, G = 0.5. P = 0.47) and in January for male lambs (M1/F = 0.235 vs M1/F = 0.19, G = 1.56, P = 0.21). Male lambs were less numerous in mixed than in matriarchal groups in November (M1/F = 0.3 vs M1/F = 0.11, G = 22.4, P > 0.001) while a trend was found in November (F1/F = 0.315 vs F1/F = 0.22, G = 4.2, P = 0.04) and a significant difference in January (F1/F = 0.33 vs F1/F = 0.25, G = 5.13. P = 0.02) in the case of female lambs.

Group size

The χ^2 tests reveal no significant difference between predicted and observed frequencies of group size distributions. So, the truncated negative binomial distributions fit the monthly group size distributions well. The parameters of these distributions are summarized in the table.

Table 1. **Estimated parameters of the monthly truncated negative binomial distributions**

Parameter	October	November	December	January
k	1.000	1.413	4.196	3.138
p	1.865	2.470	1.282	2.115
Exp.	2.865	4.217	5.554	6.831
Var.	5.341	11.570	11.710	19.960
χ^2	8.925	12.390	20.020	23.960
df	10	11	15	17

k: shape parameter, *p:* scale parameter, *Exp.:* expectations, *Var.:* variances, χ^2: chi-square, *df:* degrees of freedom.

The mouflons had an increasing tendency to aggregate from October to January. In October, animals were frequently seen alone but most were in groups of 2 to 5 individuals (mean = 2.87 ± 0.64). In November the proportion of solitary mouflons decreased and almost no single animals were seen by January. At the same time, the large groups (> 10 animals) were more numerous; the estimated mean group size gradually rose from 4.2 (± 0.91) to 6.8 (± 0.99), reflecting the flexibility of the associations.

Social tendencies and group types

Social tendencies were defined as the tendencies of each age/sex class to join a particular group type (Bon and Campan 1989).

In summer, the rams' tendency to live in male groups increased with age (Fig. 1). As adult rams were much more difficult to observe than the ewes, matriarchal groups dominated in our samples (Fig. 2).

From summer to January, the social tendencies of yearling males changed little with an obvious trend to join ewe groups (Fig. 3). Conversely, older rams changed their grouping patterns. Two-year-old males exhibited similar tendencies to yearlings from October to January. At the end of the summer, adult male groups disbanded and rams were frequently alone in October and November. Males over 7 years old were alone in over 30 % of their

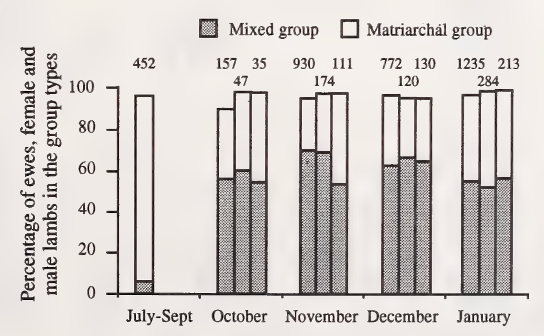


Fig. 1. Monthly percentages of adult females, female and male lambs seen in mixed and matriarchal groups during rut. Numbers of animals are indicated above columns

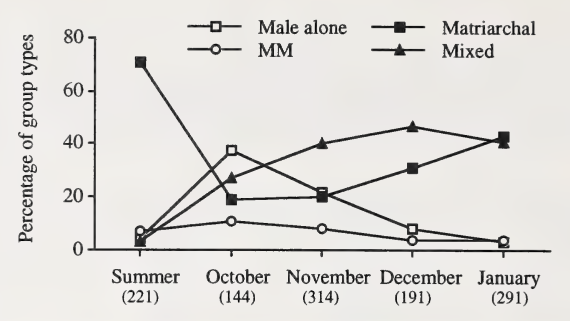


Fig. 2. Monthly percentages of group types during rut. Numbers in brackets indicate sample sizes

observations, but mature rams associated mostly with ewes so the proportion of mixed groups increased (Fig. 2).

Males over 7 years old left the female ranges after November. The younger males were almost never observed alone in December and January and more than 80 % of those which still stayed on rutting grounds lived in mixed groups.

During the rut, almost 100 % of the lambs observed associated closely with ewes. No significant differences were found between sexes about distribution in matriarchal and mixed groups except in November when male lambs were more often in matriarchal groups than female lambs (G = 6.75, P 0.009). Female lambs followed a pattern of distribution in mixed and matriarchal groups very similar to that of ewes (Fig. 1).

Fig. 3. Monthly percentages of males of each class, alone in male and in mixed groups during rut

Discussion

The advantage of adjusting the data to a truncated negative binomial distribution lies in the extension of the results given by the sample to the whole population. Such a distribution reflects the non-random association of mouflons. It provides the estimates of the parameters from which expectation and variance are issued. The expectation represents the mean group size which can be compared monthly. Indeed these comparisons could not be theoretically possible in using the empirical estimates of the mean and variance because of the monthly variation of the observed sample size.

Up to September, mature rams and ewes socially segregated as reported in wild sheep living under a seasonal climate outside the rut. During the pre-rut in October, large rams, either solitary or in small groups (Hogg 1987) enter the breeding areas and look for receptive ewes (Geist 1971; Grubb 1974; Leslie and Douglas 1979; Festa-Bianchet 1986; Van Vuren and Coblentz 1989) as observed for male ungulates (ibexes *Capra ibex* and *Walia ibex:* Nievergelt 1974; elk *Cervus elaphus canadensis;* African elephant *Loxondonta africana:* Barnes 1982; Poole 1989; feral goat *Capra hircus:* O'Brien 1984). Rams exhibit an increasing tendency to associate with ewes. The youngest rams for their part exhibit an intermediate social pattern as they still often associate with ewes (Geist 1971; Festa-Bianchet 1986, 1991). Females and juvenile live in small groups in woodland for a large part of the day, due to high temperatures, explaining the strong ram-biased sex ratio observed in October (Leslie and Douglas 1979).

In November, all animals increased their use of open areas. The proportion of ewes increased, explaining the ewe-biased sex ratio. Adult rams are often alone in search of receptive ewes. Most mouflons are observed in mixed sex groups.

The decrease in the proportion of lambs observed during rut coincides with the mating peak. Male lambs appeared more disturbed than females since during the full rut they obviously avoided the mixed groups possibly because of the presence of mature rams. It has been already found that reproductive males may repel male offspring or yearlings in Soay sheep *Ovis aries* (Grubb and Jewell 1966), impala *Aepyceros melampus* (Jarman and Jarman 1973, 1974) and wild boar *Sus scrofa* (Dardaillon 1989).

In December, the oldest rams leave the rutting grounds, spending less time with females than younger rams (Geist 1971; Geist und Petocz 1977; Leslie and Douglas 1979; Gonzalez 1985) like in other polygamous ungulates (Nievergelt 1974; Franklin and Lieb 1979; Dunbar and Dunbar 1981). Since 80 % of lambs are conceived in November (Bon et al. 1993), the presence of the oldest rams coincides with the conception peak, while younger males remain longer and serve some ewes in late œstrus (Cugnasse 1982; Bon et al. 1993) as reported by Heimer et al. (1984) in Dall sheep *(O. dalli).* The reobservation of male lambs in December and their similar rate of occurrence in mixed and matriarchal groups indicate a reduction of mating activities. This also suggests their higher independence relative to female offspring (Grubb 1974) which followed a social pattern rather similar to that of ewes.

Beginning in October, mean group size increased, possibly because of higher food availability and by the increased use of open habitats. However, the large groups observed in December and January are unexpected because food is scarce (Bon et al. 1990). Some other causes linked to reproductive activities may lead mouflons to gather. Various authors have already noted such large gatherings in other ungulates (bison *Bison bison:* Lott 1981; aoudad: Gray and Simpson 1982; bharal *Pseudois nayaur:* Wilson, 1984; wild boar: Dardaillon, 1989; Bon et al. 1990). Male wild sheep do not herd females (Geist 1971; Hogg 1984, 1987; Cavallini 1987) and we have previously shown that even in matriarchal groups the mean number of ewes rises (Bon et al. 1990). In November, reproductive activities such as competitive behaviour among rams, the temporary departure of lambs and the isolation of ewes in œstrus could cause the groups to split, despite the grouping

tendency of non-reproductive animals. This social instability may reduce the aggregative trend that we observed later. The tendency for males ≤ 6 years old to remain with ewes after the rut (Geist 1971; Bon and Campan 1989) during a period of higher social stability (Geist 1971) may explain the increasing mean group size as reported by Rounds (1980) in the post-rut for wapiti. The reduction of available and favourable habitats in winter may also partly explain the high aggregation tendency (Bon et al. 1990).

Acknowledgements

We are grateful to R. Campan, L. Arias De Reyna, P. Recuerda, L. Fattorini, and M. Festa-Bianchet for their helpful comments on earlier drafts of the manuscript. We also thank D. Dubray and J. M. Cugnasse of the Office National de la Chasse for the full facilities they gave us to achieve the field work. We are grateful to K. Kováts and C. Sperisen who kindly translated the abstract. This work was supported by a grant from the Spanish and French Foreign Offices to R. Bon, and a French-Spanish project of university cooperation.

Zusammenfassung

Dynamik der sozialen Gruppierung von Mufflons (Ovis ammon) während der Brunst

Das Gruppierungsverhalten von Mufflons während der Brunstzeit von Oktober bis Dezember wurde in Bezug auf die Anwesenheit von männlichen Tieren untersucht. Vor der Brunst waren ältere männliche Tiere zu einem hohen Grad von weiblichen Tieren getrennt. Während der Brunst folgte die Verteilung der monatlichen Gruppengröße einer abgeflachten negativen Binomialverteilung. Im Oktober lebten die Mufflons in kleinen Gruppen, und männliche Tiere betraten das Streifgebiet von weiblichen Tieren. Während einzelne erwachsene, vor allem ältere Widder, auf der Suche nach brünstigen Muttertieren waren, lebten jüngere Widder vor allem mit Mutterschafen in bewaldeten Gebieten. Zu dieser Zeit war das Verhältnis von männlichen zu weiblichen Tieren mit einem systematischen Fehler der männlichen Tiere behaftet. Im November hielten sich die Mufflons vor allem in offenen Gebieten auf. Das Geschlechterverhältnis nahm ab, während die Gruppengröße zunahm. Die männliche Population zeigte ein niedriges Verhältnis von älteren Widdern zu empfänglichen weiblichen Tieren. Wir nehmen an, daß die Reproduktionsaktivitäten die Gruppierungstendenz verzögerten, und daß dies eine hohe soziale Instabilität zur Folge hatte: Die Anwesenheit von erwachsenen männlichen Tieren bewirkte eine Auflösung von Mutter-Lamm-Bindungen während der intensivsten Periode der Paarungszeit. Männliche Lämmer schienen stärker gestört als weibliche, aber jene kehrten früher zu den Mutterschafsgruppen zurück. Im Dezember wurden selten über 6 Jahre alte männliche Tiere in Gesellschaft von weiblichen Tieren beobachtet, während jüngere Widder bis Januar bei den Mutterschafen blieben. Während dieser Periode bildeten die Mufflons häufig große Gruppen.

References

Barnes, R. F. N. (1982): Mate searching behaviour of elephant bulls in a semiarid environment. Anim. Behav. **30**, 1217–1233.

Bon, R.; Campan, R. (1989): Social tendencies of the Corsican moufflon in the Caroux-Espinouse massif (South of France). Behav. Process. **19**, 57–78.

Bon, R.; Dardaillon, M.; Estevez, I. (1993): Mating and lambing periods as related to age of female mouflons. J. Mammalogy (in press).

Bon, R.; Gonzalez, G.; Bosch, M. L.; Cugnasse, J. M. (1992): Ram rut-involvment in a hunted population of mouflons. Acta Theriol. **37**, 63–71.

Bon, R.; Gonzalez, G.; Im, S.; Badia, J. (1990): Seasonal grouping in female moufflons in relation to food availability. Ethology **86**, 224–236.

Cavallini, P. (1987): On the behaviour of male Sardinian moufflons *(Ovis orientalis musimon)* during the pre-rut. Mammalia **51**, 195–200.

Cugnasse, J. M. (1982): Evolution démographique des mouflons dans le Massif du Caroux. Bull. mens. ONC **59**, 24–32.

Cugnasse, J. M.; Garcia, M.; Veyrac, T. (1985): Contribution à l'étude de la biologie de la reproduction du Mouflon *(Ovis ammon musimon)*, par examen post-mortem, dans le massif du Caroux-Espinouse. Bull. mens. ONC **89**, 33–35.

Dardaillon, M. (1989): Wild boar social groupings and their seasonal changes in the Camargue, southern France. Z. Säugetierkunde **53**, 22–30.

Dunbar, R. I. M.; Dunbar, E. P. (1981): The grouping behaviour of male *Walia ibex* with special reference to the rut. Afr. J. Ecol. **19**, 251–263.

FESTA-BIANCHET, M. (1986): Site fidelity and seasonal range use by bighorn rams. Can. J. Zool. **64**, 2126–2132.
— (1991): The social system of bighorn sheep: grouping patterns, kinship and female dominance rank. Anim. Behav. **42**, 71–82.
FRANKLIN, W. L.; LIEB, J. W. (1979): The social organization of a sedentary population of North American elk: a model for understanding other populations. In: North American Elk: Ecology, Behaviour and Management. Ed. by M. S. BOYCE and L. D. HAYDEN-WING. New York: Laramie. Pp. 185–198.
GEIST, V. (1971): Mountain sheep. Chicago: Chicago University Press.
GEIST, V.; PETOCZ, R. G. (1977): Bighorn sheep in winter: do rams maximize reproductive fitness by spatial and habitat segregation from ewes? Can. J. Zool. **55**, 1802–1810.
GONZALEZ, G. (1985): Les groupes sociaux d'isards et de mouflons, au massif du Carlit (Pyrénées Orientales). Gibier Faune Sauvage **4**, 85–102.
GRAY, G. G.; SIMPSON, C. D. (1982): Group dynamics of free-ranging Barbary sheep in Texas. J. Wildl. Manage. **46**, 1096–1101.
GRUBB, P. (1974): Mating activity and the social significance of rams in a feral sheep community. In: The Behaviour of Ungulates and its Relation to Management. Ed. by V. GEIST and F. WALTHER. Morges, Switzerland: IUCN No. **50**. Pp. 457–476.
GRUBB, P.; JEWELL, P. A. (1966): Social grouping and home range in feral Soay sheep. Symp. Zool. Soc. Lond. **18**, 179–210.
— — (1974): Movement, daily activity and home range of Soay sheep. In: Island Survivors: the Ecology of the Soay sheep of St. Kilda. Ed. by P. A. JEWELL, C. MILNER, and J. M. BOYD. London: Athlone Press. Pp. 224–241.
HEIMER, W. E.; WATSON, S. M.; SMITH, III T. C. (1984): Excess ram mortality in a heavily hunted Dall sheep population. Symp. North Wild Sheep and Goat Counc. **4**, 425–432.
HOGG, J. T. (1984): Mating in bighorn sheep: multiple creative male strategies. Science **225**, 526–529.
— (1987): Intrasexual competition and mate choice in Rocky mountain bighorn sheep. Ethology **75**, 119–144.
JARMAN, P. J.; JARMAN, M. V. (1973): Social behaviour, population structure and reproductive potential in impala. E. Afr. Wildl. J. **11**, 329–338.
— — (1974): Impala behaviour and its relevance to management. In: The Behaviour of Ungulates and its Relation to Management. Ed. by V. GEIST and F. WALTHER. Morges, Switzerland: IUCN No. **50**. Pp. 871–881.
JOHNSON, L. J.; KOTZ, S. (1969): Discrete distributions. New York: John Wiley and Sons.
LESLIE, D. M.; DOUGLAS, C. L. (1979): Desert Bighorn sheep of the River Mountains, Nevada. Wildl. Monogr. **66**, 1–56.
LOTT, D. L. (1981): Sexual behaviour and intersex strategies in American bison. Z. Tierpsychol. **56**, 97–114.
NIEVERGELT, B. (1974): A comparison of rutting behaviour and grouping in the Ethiopian and alpine ibex. In: The Behaviour of Ungulates and its Relation to Management. Ed. by V. GEIST and F. WALTHER. Morges, Switzerland: IUCN No. **50**. Pp. 324–340.
O'BRIEN, P. H. (1984): Feral goat home range: influence of social class and environmental variables. Appl. Anim. Behav. Sci. **12**, 373–385.
PFEFFER, P. (1967): Le mouflon de Corse (*Ovis ammon musimon* Schreber, 1782), Position systématique, écologie et éthologie comparées. Mammalia **31**, 1–262.
POOLE, J. H. (1989): Mate guarding, reproductive success and female choice in African elephants. Anim. Behav. **37**, 842–849.
ROUNDS, R. C. (1980): Aggregation behavior of wapiti *(Cervus elaphus)* in Riding Mountains National Park, Manitoba. Can. Field-Nat. **94**, 148–153.
SQUIBB, R. C. (1985): Mating success of yearling and older bull elk. J. Wildl. Manage. **49**, 744–750.
VUREN D. VAN; COBLENTZ, B. E. (1989): Population characteristics of feral sheep on Santa Cruz Island. J. Wildl. Manage. **53**, 306–313.
WILSON, P. (1984): Aspects of reproductive behaviour of bharal *(Pseudois nayaur)* in Nepal. Z. Säugetierkunde **49**, 36–42.

Authors' addresses: RICHARD BON, Université de Sherbrooke, Faculté des sciences, Sherbrooke, Quebec, Canada J1K 2R1; MARIE LINE MAUBLANC, Institut de Recherche sur les Grands Mammifères, Institut National de la Recherche Agronomique, BP 27, F-31326 Castanet Tolosan Cedex, France; JACQUES BADIA, Station de Biométrie et d'Intelligence Artificielle, Institut National de la Recherche Agronomique, BP 27, F-31326 Castanet Tolosan Cedex, France; JOSE MIGUEL RECARTE, Departamento de Biologí Animal (Etología), Facultad de Ciencias, Avda. San Alberto Magno s/n., E-14604 Cordoba, Spain

Z. Säugetierkunde 58 (1993) 302–311

ISSN 0044-3468

Effects of food abundance and habitat structure on seed-eating rodents in Spain wintering in man-made habitats

By M. Díaz, Elvira Gonzalez, R. Muñoz-Pulido, and M. A. Naveso

Departamento de Biología Animal I, Facultad de Biología, Universidad Complutense, and Museo Nacional de Ciencias Naturales, Madrid, Spain

Receipt of Ms. 5. 6. 1992
Acceptance of Ms. 10. 3. 1993

Abstract

The patterns of abundance and seed (acorn) predation rates were analyzed in granivorous rodents (mainly the wood mouse *Apodemus sylvaticus* L.) wintering in two man-made habitats: cereal croplands, and a kind of wood-pasture exclusive to the western Mediterranean basin, the dehesas. Both seed (acorn) abundance and vegetation structure were also measured. Within dehesas, neither rodent abundance nor acorn predation rates were related to acorn abundance, whereas there was a significant association between rodent abundance and shrub cover at the end of winter. These results were coincident with previous findings in croplands. Both rodent abundances and seed predation rates were lower in dehesas than in croplands, despite the better structural and trophic conditions of the first habitat for rodents (larger shrub cover and food abundance). However, the body condition of animals was better in dehesas, to the extent that we found strong evidence for winter reproduction. Rodent predator communities appear to be more diverse and denser in dehesas than in croplands. This suggests a heavier predation pressure in dehesas which would have culled rodent populations in such a way that food was plentiful for survivors, thus explaining their scarcity, good body condition, and low dependence on food resources.

Introduction

Patterns of rodent abundance and seed predation rates have been intensively studied in the last few years, focussing mainly on deserts throughout the entire world (Brown et al. 1975; Mares and Rosenzweig 1978; Abramsky 1983; Morton 1985). Experimental studies have shown that seed availability (Price and Waser 1985), shrub cover (Brown 1988) and moonlight levels (Kotler et al. 1991; Longland and Price 1991) are the main factors influencing desert rodent abundance and seed predation patterns by their effect on food intake rates and predation risk (Simonetti 1989). In man-modified habitats such as cereal croplands, however, a recent study (Díaz 1992) showed that seed abundance was of minor importance to seed-eating rodents (mainly the wood mouse *Apodemus sylvaticus* L.). This seems to be caused by the strong demand by rodents for safe refuges and foraging sites during winter (Díaz 1992).

The aim of this study is to analyse the winter patterns of abundance and seed (acorn) predation rates of rodents inhabiting a kind of wood-pasture exclusive to the western Mediterranean basin, the dehesas (Campos and Martin 1987). This man-modified habitat consists of cleared oak woodlands with open grasslands and Mediterranean scrub. Their management (tree clearing, cereal sowing, and shrub removal by ploughing) produces a mosaic of plots that differ in soil and understory vegetation characteristics (stability, herb and shrub cover) in a similar way to croplands (Díaz 1992), so that we can compare the results obtained with the findings outlined above.

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5805-0302 $ 02.50/0

Material and methods

Study area

Data were collected in the Tiétar valley, 15 km SW of Candeleda (40° 06′ N, 05° 17′ W, about 300 m a.s.l.), central Spain. The climate is humid Mediterranean with hot summers and mild winters (Ministerio de Agricultura 1981). The study area is covered mainly by holm oak *Quercus ilex* L. dehesas, with some interspersed cork oak *Q. suber* L. and ash *Fraxinus excelsior* L. trees growing along seasonal streams. The main shrub species are *Crataegus monogyna* Jacq., *Lavandula stoechas* L., *Halimium ocymoides* (Lam.) Willk., *H. viscosum* Willk., and saplings of the dominant tree species. The herb layer is composed mainly of *Trifolium* spp., *Ornithopus compressus* L., *Vulpia* spp., *Poa bulbosa* L., *Tuberaria guttata* (L.) Fourr., and *Leontodon* spp. Small plots sowed with cereals (mainly oats *Avena sativa* L. and rye *Secale cereale* L.) are also present.

Sampling design

Twelve 500 × 100 m plots were established in the study area. Four of them were ploughed and sowed with oats and rye in September 1990, four had been intensively grazed by sheep and cattle during the last ten years, and four had not been ploughed in the last twenty years and were only lightly grazed by cattle. The plots were selected to represent these three management types of dehesas (hereafter called cultivated, grazed, and shrubby dehesas, respectively; see Campos and Martin 1987), and they were located forming pairs or trios in contact zones between management types whenever possible.

On each plot, we marked twenty holm oak trees in October 1990, under whose canopies we carried out acorn censuses and measured rodent acorn predation rates. Holm oaks were selected by walking a 500 m transect along the middle of the plot, and marking the nearest tree at either side of the progression line at 25 m-intervals. In March 1991 we selected twenty additional trees in each plot for rodent trapping. Each of them was located between each pair of consecutive trees previously chosen, plus one more located at approximately 15 m from the last marked tree.

Acorn abundance

We established two 0.5 × 0.5 m permanent squares under the canopy of each of the 240 trees marked in October 1990. The positions of the squares were chosen at random following the procedure proposed by Skalski (1987). The diagonal of each square was marked by means of two nails pinned in the ground. We counted the holm oak acorns present within a square iron frame placed between each pair of nails. Acorn censuses started with one count made in late October 1990, and then continued at two week intervals from late November 1990 to mid March 1991.

Rodent predation rates

The impact of rodents on acorns was assessed in December 1990, January 1991, and February 1991. The acorns present in the permanent squares were counted at dusk and at dawn of one sampling night per month, corresponding to the dark moon phase to eliminate the effect of moonlight on rodent foraging activity (Kotler et al. 1991; Longland and Price 1991). The difference between these two counts was assumed to be the number of acorns taken by rodents during one night, since no other nocturnal acorn predators (red deer *Cervus elaphus* L., wild boar *Sus scrofa* L.) were noticed in the study plots. Results of the dusk censuses were also used as an estimate of the acorn abundance at these dates. Acorn predation rates were not measured in October and November because acorns were still falling from the trees at these dates.

Vegetation structure

Vegetation structure of each study plot was quantified by use of 100 scored sticks that were placed vertically on the ground at 5 m intervals over a line transect. We used the stick to assess whether vegetation was contacted at 10 cm-height intervals from the ground level to 1 m height or more; if positive, the life form (herb or shrub) of the plant(s) contacted was noted. We also considered the presence or absence of leaf litter, stones or bare ground at the 0 cm level (see e.g. Díaz and Carrascal 1991). This technique provided detailed descriptions of the structure of the vegetation based on objective percentage covers (number of positive contacts out of the 100 sample points). The height of the understory vegetation was also measured at each sample point by noting the highest plant contact with the stick to the nearest 5 cm. All these measurements were taken in November–December 1991, just before winter freezing temperatures interrupt vegetation growth until next spring (Perez 1988). Tree cover was estimated by counting the number of trees on aerial photographies of

the study plots, and then computing their cover by assuming a mean canopy radius of 6 m (N = 76 trees; SE = 0.2 m). We then performed a Principal Component Analysis (see THOMPSON et al. 1991 for a similar approach) on these data to reduce the number of structural variables with a minimum loss of information. Since we only took twelve measures, we had to reduce the set of variables before analysis. This was done by pooling the covers of bare ground, litter and stones in an "unvegetated ground cover" variable, and by considering the herb and shrub covers in only three height intervals (0, 0–50, and >50 cm height).

Rodent abundance

Rodent abundance in each plot was estimated in March 1991. Two snap-traps were placed close to the trunk of each of the forty holm oak trees per plot reviously selected. Trapping started on 9th March and lasted three consecutive dark moonlit nights. All the rodents caught were identified to the species level, weighed, and dissected to determine sex, reproductive state (testes enlarged or not in males, and lactancy or pregnancy in females), and body size (measured as condylo-basal length of the skull; ALCANTARA and DÍAZ 1993).

Results

Vegetation structure

Cultivated plots were characterized by their large covers of bare ground, and of herbaceous plants at 0–50 cm height. Grazed plots showed large herb covers at the ground level, but these covers decreased sharply as height increased, thus giving the shortest mean vegetation heights. Finally, shrubby plots showed the tallest mean vegetation heights, as well as large shrub covers between 0 and 50 cm in height (Tab. 1). The first principal component

Table 1. **Average (±SE) values of vegetation structure variables according to the management type of study plots, and correlation coefficients between those variables and the two first factors obtained in the Principal Component Analysis of vegetation structure**

Variable	cultivated	grazed	shrubby	PC I	PC II
Total cover of herbs (%)	84.0 ± 8.7	76.8 ± 13.0	73.5 ± 4.9	0.418	0.182
Total cover of shrubs (%)	0.0 ± 0.0	1.0 ± 0.8	36.0 ± 14.3	–0.988**	0.041
Cover of trees (%)	23.6 ± 9.3	23.8 ± 9.4	22.7 ± 10.5	–0.152	–0.108
Cover of unvegetated ground (%)	54.0 ± 16.2	25.0 ± 11.5	32.3 ± 3.9	0.323	0.842**
Cover of herbs at > 50 cm height (%)	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.5	–0.659**	0.094
Cover of herbs at 0–50 cm height (%)	23.0 ± 16.4	6.5 ± 3.3	15.8 ± 6.7	0.269	0.822**
Cover of herbs at 0 cm height (%)	83.8 ± 8.3	76.0 ± 12.6	70.8 ± 3.9	–0.245	–0.866**
Cover of shrubs at > 50 cm height (%)	0.0 ± 0.0	0.0 ± 0.0	11.0 ± 6.7	–0.933**	0.169
Cover of shrubs at 0–50 cm height (%)	0.0 ± 0.0	0.5 ± 0.6	25.5 ± 10.5	–0.981**	0.033
Cover of shrubs at 0 cm height (%)	0.0 ± 0.0	0.8 ± 1.0	17.5 ± 4.7	–0.823**	0.099
Mean vegetation height (cm)	12.9 ± 3.3	4.7 ± 1.5	38.3 ± 17.3	–0.733**	0.581
Eigenvalue				4.89	2.57
% variance				44.5	23.3
Σ % variance					67.8

* = $p < 0.05$; ** = $p < 0.01$. $df = 10$.

obtained in the analysis of these variables is an inverse gradient of shrub cover and vegetation height, and it segregates the shrubby plots from those grazed or cultivated (Tab. 1, Fig. 1). The second component segregates the plots according to the structure of their herb layer. It correlates positively with herb cover at 0–50 cm and with the cover of unvegetated ground, and negatively with herb cover at the 0 cm level; hence it segregates cultivated plots from grazed ones (Fig. 1).

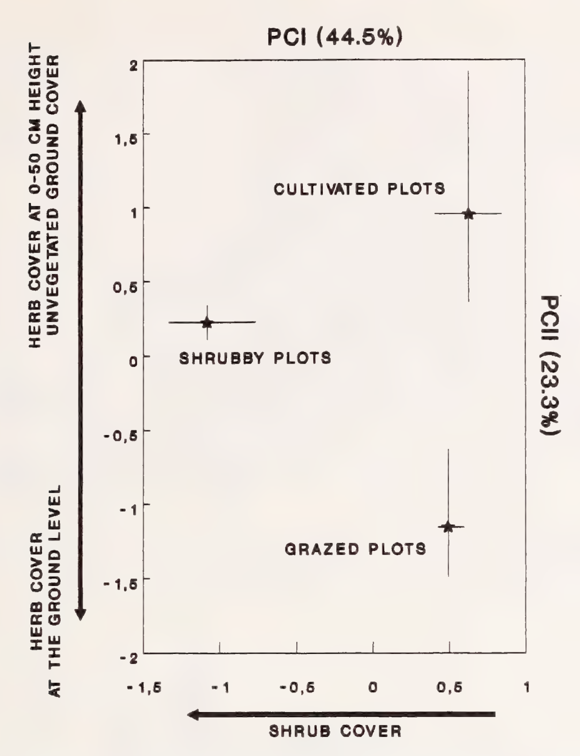


Fig. 1. Mean coordinates of the three management types of plots (N = 4 for each management type; lines show ranges) in the plane defined by principal components I and II of the analysis of vegetation structure. Both percent variances explained and the interpretation of each component are also shown

Acorn abundance

Mean acorn abundances ranged between 26.08 per m^2 in cultivated plots in December and 0.75 acorns m^{-2} in grazed plots in March. A three-way ANOVA analysis on log-transformed numbers of acorns per square (average values of the two squares under each tree) showed highly significant effects ($p < 0.001$) of both plot, type of management and sampling date. There were also significant plot-habitat and date-habitat interactions. The plot-date interaction, as well as the three-way interaction term, were not significant, i.e. the mean acorn abundances showed changing patterns of spatial and temporal variability, whereas the trends showed by each plot were constant over time. Cultivated plots had on average larger acorn abundances than grazed and shrubby ones at any sampling date, except at the late October census. Peak acorn abundances were not synchronized in the three management types; they were reached in late November in shrubby plots, in mid December in grazed ones, and in late December in cultivated ones (Fig. 2).

Rodent abundance and acorn predation rates

We captured 30 rodents (18 wood mice *Apodemus sylvaticus* L., 2 Algerian mice *Mus spretus* Lataste, and 10 garden dormice *Eliomys quercinus* L.) in 2880 trap-nights (240 trap-nights per plot; Fig. 3). Overall trapping success differed between species only when the analysis was carried out over the whole data base (fit of log-linear models to the four-way contingency table generated by the factors plot × management type × species × presence/

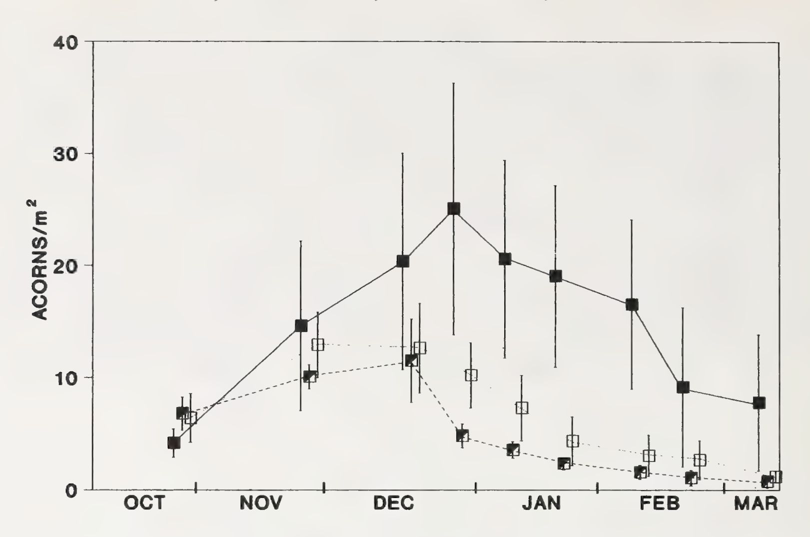


Fig. 2. Mean (± SE) numbers of acorns m^{-2} according to sampling date and the management type of plots (filled squares: cultivated; half-filled squares: grazed; empty squares: shrubby). N = 4 by each management type, except for cultivated and grazed in late December, when only three plots of each could be censused

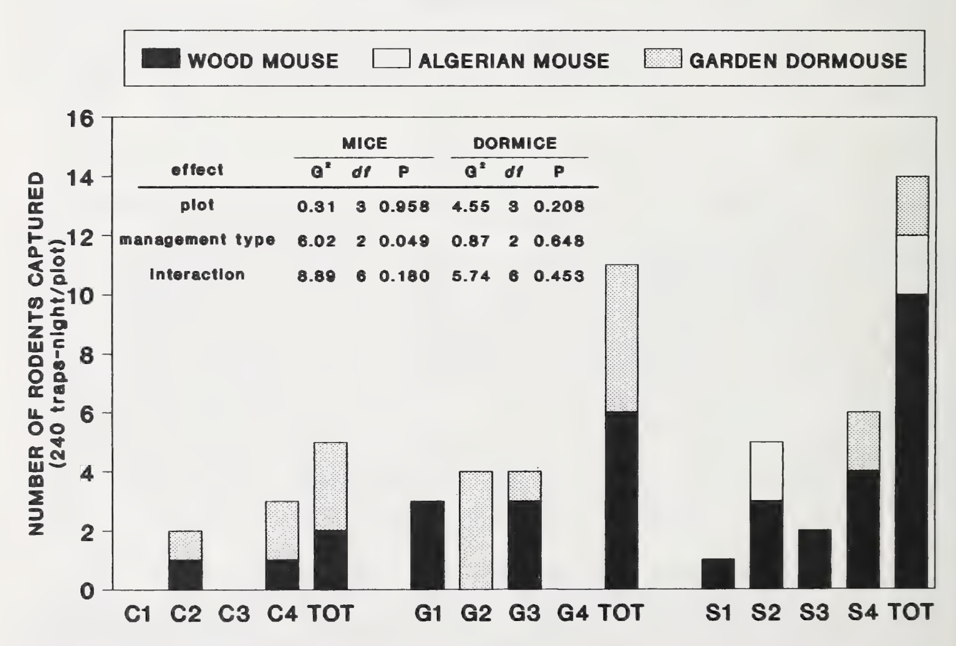


Fig. 3. Rodent captures of each species in each study plot (C1–4: cultivated; G1–4: grazed; S1–4: shrubby). Results of the fit of log-linear models (Sokal and Rohlf 1981; Heisey 1985) for the three-way contingency tables generated by the factors plot × management type × presence/absence of capture are also shown for each rodent species (both mice grouped for analysis)

absence of capture [Sokal and Rohlf 1981; Heisey 1985]; $G^2 = 8.42$, $P = 0.015$, df = 2 for the species effect; $P > 0.2$ for the effects of the remaining factors and factor interactions). However, when the analyses were carried out separately for each rodent species (both mice species pooled because of their quite similar foraging behaviour; see Díaz 1992), a significant effect of plot management on mice abundance was detected. Mice were most abundant in shrubby plots and least abundant in cultivated ones, whereas dormice abundance was not affected by this factor (Fig. 3). This latter species hibernates from November to March in central Spain (Palacios 1974), so it is unlikely that the animals captured were active when acorn predation rates were measured. Moreover, this species is mainly arboreal, so that it is unlikely that the soil and understory modifications considered here would affect its populations. Thus, we will not further consider the garden dormice.

The number of acorns taken by rodents per square meter decreased significantly from the beginning of winter onwards (Fig. 4), the spatial pattern of this variable being, however, statistically indistinguishable from evenness (three-way ANOVA on the average number of acorns taken from the two quadrats located under each marked tree, log-transformed; $F_{2,674} = 7.25$, $P < 0.001$ for the effect of sampling date, $p > 0.05$ for the effects of plot, plot management, and all factor interactions).

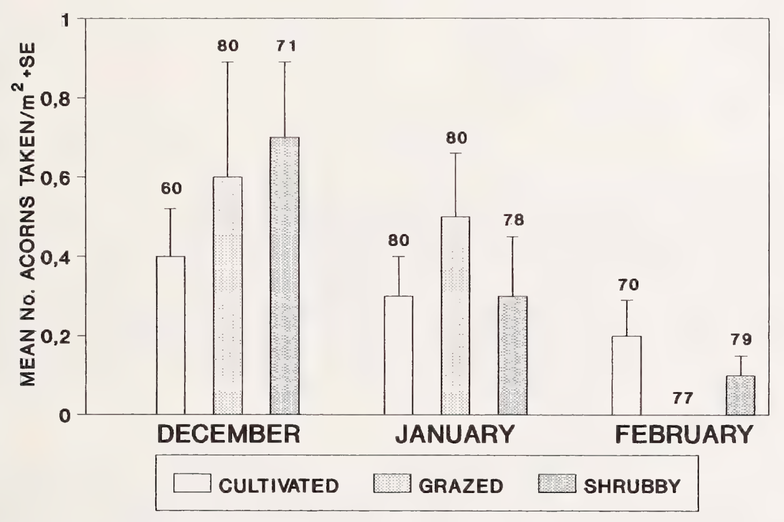


Fig. 4. Average acorn predation rates according to sampling date and the management type of plots. The figures over the bars indicate the number of oak trees sampled

Mice abundance was significantly correlated with shrub cover (inverse of PCI; $r = -0.62$, $P < 0.05$, $N = 12$ plots), but not with acorn abundance or with the characteristics of the herb layer (PCII). The correlation coefficients between mice abundance and rodent predation rates were not significant. Rodent predation rates were not correlated with any structural gradient or with acorn abundance at any sampling date.

Comparisons with cereal croplands

Results obtained show (Tab. 2) that both mice abundance and rodent seed predation rates were larger in croplands than in dehesas (about 4.5 and 6 times larger, respectively). Both average shrub cover and food abundance were, however, much larger in dehesas than in croplands (12 times larger for cover, and about one order of magnitude larger for food abundance, even without considering any other seed but acorns in dehesas). The average

Table 2. **Comparisons of average mice abundances, rodent seed predation rates, body mass, body size, and body condition of mice populations wintering in cereal croplands (from Díaz 1992) and in dehesas**

Average food abundance and shrub cover of both habitat types are also shown. See Appendix for the methods used to reduce these variables to common, comparable units

	Dehesas	Croplands	
Rodent abundance (rod./100 trap-nights)	0.69 (N = 2880)	3.14 (N = 1052)	$G_1 = 29.9^{***}$
Seed predation rates (% seeds preyed upon)	2.91 (N = 1222)	18.60 (N = 264)	$G_1 = 68.1^{***}$
Body mass (g; $\bar{X} \pm SE$)	26.3 ± 2.5 (N = 12)	18.2 ± 0.5 (N = 26)	$F_{1,36} = 20.1^{***}$
Body size (CBL) (mm; $\bar{X} \pm SE$)	23.6 ± 0.3 (N = 12)	23.1 ± 0.2 (N = 26)	$F_{1,36} = 1.9^{n.s.}$
Body condition ($\bar{X} \pm SE$)	2.0 ± 1.4 (N = 12)	−0.1 ± 0.1 (N = 26)	$F_{1,36} = 5.2^{*}$
Food abundance (kJ seeds/ha)	1.6×10^6	2.6×10^5	
Shrub cover (%) ($\bar{X} \pm SE$)	12.4 ± 5.5 (N = 12 plots)	0.1 ± 0.1 (N = 264)	$t_{274} = 12.1^{***}$

*** = $p < 0.001$; * = $p < 0.05$; n.s. = $p > 0.05$.

body mass of wood mice wintering in dehesas was larger than that of mice inhabiting croplands (Tab. 2); their body size, however, did not differ between these two habitats, whereas the body condition of mice was better in dehesas than in croplands (Tab. 2). Moreover, we found strong evidence for winter breeding in dehesas: 8 out of 10 male wood mice showed enlarged testes in early March and, out of 7 females, 3 were lactating, one was pregnant, and two were probably less than 9 weeks old (they both weighed less than 20 g and showed a dark grey fur; Corbet and Southern 1977; Gurnell and Knee 1984). In croplands, only 2 out of 20 males captured showed enlarged testes, and none of the 11 females were lactating or pregnant.

Discussion

Concerning their carrying capacity, dehesas seem to be a poor wintering habitat for rodents, since they support very low population densities as compared with croplands. This situation cannot be attributed to worse trophic conditions because, on the one hand, food abundance in dehesas seems to be quite large, and on the other hand, the body condition of mice inhabiting dehesas was much better than those of mice inhabiting croplands, to the extent that they could have bred during winter (winter sexual activity in rodents is mainly related to adequacy of food conditions; Clarke 1985; Hansson 1984). Moreover, neither rodent abundance nor rodent predation rates were associated to food abundance within dehesas at any date, and rodent foraging impact appeared to be too low to deplete food resources significantly.

Two other factors apart from food abundance have been postulated as being primary in regulating rodent abundance: the availability of home sites, and the effectiveness of agents affecting life-spans (Pennycuik et al. 1987). The main process affecting life-spans in small rodents seems to be predation pressure, that in turn is related to predator abundance (e.g. Steen et al. 1990) and to the availability of safe foraging places such as shrub understories. From this point of view, dehesas would have been more populated than croplands, since

they offer stable ground everywhere to build refuges (the area close to the tree trunks is never ploughed), and their average shrub cover was also larger. Contrary to these expectations, dehesas seem to maintain lower rodent population densities than croplands. Dehesas are inhabited by a diversified, and probably dense, rodent predator community (four owl species – *Tyto alba* Scopoli, *Athene noctua* Scopoli, *Strix aluco* L., and *Asio otus* L. – and four carnivore species – *Vulpes vulpes* L., *Mustela nivalis* L., *M. putorius* L., and *Genetta genetta* L.), whereas in croplands most rodent predators have been excluded by human activities (only *T. alba, A. noctua, V. vulpes*, and *M. nivalis* were present). These data, although rather qualitative, suggest that rodents in dehesas would have been subjected to a heavier predation pressure than in croplands.

Following this argument, close associations to shrubby plots within dehesas should have been found if predation risk would have been consistently important all through the winter (BROWN 1988; SIMONETTI 1989; DÍAZ 1992). This association, however, was only evident at the end of winter, whereas acorn predation rates did not show any pattern of association with vegetation structure. This result could have arisen from the fact that acorn predation rates were measured in dark moon nights only. There is both direct and indirect evidence that low levels of nocturnal illumination relax predation risk, thus permitting wide movements of rodents from daylight refuges (KOTLER et al. 1991; LONGLAND and PRICE 1991; DÍAZ 1992). These refuges could be built up even in the most heavily managed plots since the area close to the tree trunks remains unploughed. Predation pressure, however, would have culled rodent populations faster in cultivated and grazed plots, where foraging animals would have been more exposed to predators because of the scarcity or lack of protective cover, than in shrubby ones.

Summarizing, rodent populations in dehesas appeared to be maintained at low levels by the combined effect of a heavy predation pressure and a man-made scarcity of safe foraging places. This culled situation could have been the cause of the low importance of food resources in determining intra-dehesas patterns of rodent abundance and acorn predation rates. Furthermore, the lare abundance of food resources in relation to the demands of a culled population might have produced an excess of food for survivors during the winter, which could explain their good physiological condition (PENNYCUIK et al. 1987; DESY and BATZLI 1989).

Appendix

Methods used to reduce the variables considered in table 2 to common units

Seed predation rates: computed as the percentage of seed trays visited over the number available in croplands (DÍAZ 1992), and as the average percentage of acorns predated over the number available in each of the three sampling periods (December, January, and February) considered in this study.

Body condition of wood mice: residuals from the regression model relating body weight (W) and condylo-basal length (CBL): $W = 0.0005\ CBL^{3.41}$; $R^2 = 44\ \%$; $p < 0.01$; $N = 163$ wood mice wintering in a wide array of habitat types from central Spain (ALCANTARA and DÍAZ 1993).

Energy value of seeds: according to DÍAZ (1991) for croplands. For dehesas, this value was computed from the mean density of acorns in midwinter months – January and February; see figure 2 –, the average dry weight of acorns in the study area −1.48 g; N = 4941 – the mean nutrient composition of holm oak acorns – see HERRERA (1977) –, and the caloric values of proteins, fats, and carbohydrates given by GLÜCK (1985).

Shrub cover in croplands: measured on 1-m^2 sampling plots around each seed tray (see DÍAZ 1992). Data arcsin-transformed before analysis.

Acknowledgements

J. DE BÁRCENA, J. VELASCO and J. L. GARCÍA kindly allowed us to perform the field work on their land. We wish to thank PALOMA, GUSTAVO, MANOLO, MENCHU, JUAN, and especially ANA and SUSY, for their valuable assistance during field work. M. ALCÁNTARA, J. A. DÍAZ, T. SANTOS, J. L. TELLERÍA and J. NELSON reviewed earlier drafts of the manuscript. M. D. was funded by a PFPI grant from the Spanish Ministerio de Educación y Ciencia, and R.M.P. by a grant from the Spanish Consejo Superior de Investigaciones Científicas, while performing this study.

Zusammenfassung

Auswirkungen von Nahrungsüberfluß und Habitatstruktur auf Körner fressende Rodentia, die in Spanien in von Menschen geschaffenen Lebensräumen überwintern

Die Studie analysiert die Auswirkungen von Überfluß an Getreidekörnern und Eicheln auf Körner fressende Nagetiere, die in von Menschen geschaffenen Habitaten überwintern (hauptsächlich Feldmäuse, *Apodemus sylvaticus* L.). Es geht um zwei verschiedene Lebensräume: Getreidefelder und lichte Steineichenwälder im Westen Spaniens, dehesas genannt. In den dehesas wurde kein Zusammenhang zwischen den großen Mengen an Eicheln und einer möglichen Überpopulation an Nagern festgestellt. Die große Nagerpopulation im Winter ist eindeutig auf den dichten Buschbestand zurückzuführen. Dieses Ergebnis stimmt mit vorherigen Studien überein. Obwohl die dehesas den Nagern bessere Lebens- und Nahrungsbedingungen bieten, ist die Anzahl der Nager geringer als in den Getreidefeldern. Die Nager der dehesas sind jedoch in einem besseren körperlichen Zustand als ihre Artgenossen in den Getreidefeldern; sie vermehren sich sogar im Winter. Außerdem scheinen die Nagerpopulationen der dehesas dichter und vielseitiger zu sein. Die relativ geringe Anzahl an Nagern trotz besserer Lebenskonditionen ist nur dadurch zu erklären, daß die Populationen durch den erhöhten Druck von Raubtieren dezimiert werden. Den überlebenden Nagern steht so ein reichhaltiges Nahrungsangebot zur Verfügung, Grund für ihre gute körperliche Verfassung und ihre weitgehende Unabhängigkeit von speziellen Nahrungsquellen.

References

Ministerio de Agricultura (1981): Mapa de Cultivos y Aprovechamientos. Villanueva de la Vera. Madrid: Ministerio de Agricultura.

Abramsky, Z. (1983): Experiments on seed predation by rodents and ants in the Israeli desert. Oecologia **57**, 328–332.

Alcantara, M.; Díaz, M. (1993): Patterns of body weight, body size, and body condition in the Wood Mouse *Apodemus sylvaticus* L.: Effects of sex and habitat quality. Proc. I European Cong. Mamm. (in press).

Brown, J. H.; Grover, J. J.; Davidson, D. W.; Lieberman, G. A. (1975): A preliminary study of seed predation in desert and montane habitats. Ecology **56**, 987–992.

Brown, J. S. (1988): Patch use as an indicator of patch preference, predation risk, and competition. Behav. Ecol. Sociobiol. **22**, 37–47.

Campos, P.; Martin, M. (eds.) (1987): Conservación y desarrollo de las dehesas portuguesa y española. Madrid: Ministerio de Agricultura.

Clarke, J. R. (1985): The reproductive biology of the bank vole *(Clethrionomys glareolus)* and the wood mouse *(Apodemus sylvaticus)*. Symp. Zool. Soc. London **55**, 33–59.

Corbet, G. B.; Southern, H. N. (1977): The handbook of British mammals. 2nd. ed. London: Blackwell.

Desy, E. A.; Batzli, G. O. (1989): Effects of food availability and predation on praire vole demography: a field experiment. Ecology **70**, 411–421.

Díaz, J. A.; Carrascal, L. M. (1991): Regional distribution of a Mediterranean lizard: influence of habitat cues and prey abundance. J. Biogeogr. **18**, 291–297.

Díaz, M. (1991): Comunidades de animales granívoros en áreas de cultivo cerealista de la Península Ibérica. PhD. Thesis. Madrid: Universidad Complutense.

— (1992): Rodent seed predation in cereal crop areas of Central Spain: effects of physiognomy, food availability, and predation risk. Ecography **15**, 77–85.

Glück, E. E. (1985): Seed preference and energy intake of Goldfinches *Carduelis carduelis* in the breeding season. Ibis **127**, 421–429.

Gurnell, J.; Knee, C. I. (1984): Determining the age of wood mice *(Apodemus sylvaticus)*. Folia Zool. **33**, 339–348.

Hansson, L. (1984): Winter reproduction of small mammals in relation to food conditions and population dynamics. In: Winter ecology of small mammals. Ed. by J. F. Merrit. London: Special Publications of the Carnegie Museum of Natural History **10**, 225–234.

Heisey, D. M. (1985): Analyzing selection experiments with log-linear models. Ecology **66**, 1744–1748.

Herrera, C. M. (1977): Ecología alimentaria del Petirrojo *(Erithacus rubecula)* durante su invernada en encinares del sur de España. Doñana, Acta Vert. **4**, 35–59.

Kotler, B. P.; Brown, J. S.; Hasson, O. (1991): Factors affecting gerbil foraging behaviour and rates of owl predation. Ecology **72**, 2249–2260.

Longland, W. S.; Price, M. V. (1991): Direct observations of owls and heteromyid rodents: can predation risk explain microhabitat use? Ecology **72**, 2261–2273.

Mares, M. A.; Rosenzweig, M. L. (1978): Granivory in North and South American deserts: rodents, birds, and ants. Ecology **59**, 235–241.

Morton, S. R. (1985): Granivory in arid regions: comparison of Australia with North and South America. Ecology **66,** 1859–1866.

Palacios, F. (1974): Contribución al estudio de la biología del Lirón Careto, *Eliomys quercinus* Linnaeus 1766, en Iberia Central, Parte I: Crecimiento, reproducción y nidificación. Doñana, Acta Vert. **1,** 171–231.

Pennycuik, P. R.; Reisner, A. H.; Westwood, N. H. (1987): Effects of variations in the availability of food and home sites and of culling on populations of house mice housed in out-door pens. Oikos **50,** 33–41.

Perez, A. (1988): Cambios y problemática en la dehesa (El suroeste de Badajoz). Badajoz: Univ. Extremadura.

Price, M. V.; Waser, N. M. (1985): Microhabitat use by heteromyid rodents: effects of artificial seed patches. Ecology **66,** 211–219.

Simonetti, J. A. (1989): Microhabitat use by small mammals in central Chile. Oikos **56,** 309–318.

Skalski, J. R. (1987): Selecting a random sample of points in circular field plots. Ecology **68,** 749.

Sokal, R. R.; Rohlf, F. J. (1981): Biometry. 2nd. ed. San Francisco: Freeman.

Steen, H.; Yoccoz, N. G.; Ims, R. A. (1990): Predators and small rodent cycles: an analysis of a 79-year time series of small rodent population fluctuations. Oikos **59,** 115–120.

Thompson, D. B.; Brown, J. H.; Spencer, W. D. (1991): Indirect facilitation of granivorous birds by desert rodents: experimental evidence from foraging patterns. Ecology **72,** 852–863.

Authors' addresses: Mario Díaz, Elvira Gonzalez, and Miguel Angel Naveso, Departamento de Biología Animal I, Facultad de Biología, Universidad Complutense, E-28040 Madrid, Spain; Rodrigo Muñoz-Pulido, Museo Nacional de Ciencias Naturales, CSIC, c/José Gutiérrez Abascal 2, E-28006 Madrid, Spain. (Present address of M. A. Naveso: Sociedad Española de Ornitología. Facultad de Biología, Universidad Complutense, E-28040 Madrid, Spain)

Z. Säugetierkunde 58 (1993) 312

ISSN 0044-3468

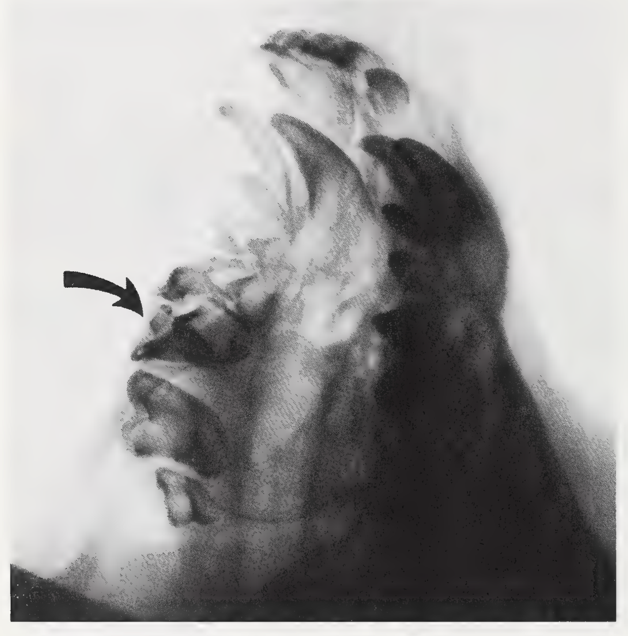
WISSENSCHAFTLICHE KURZMITTEILUNGEN

A clarification of the dental formula of *Bassariscus sumichrasti* (Carnivora; Procyonidae)

By INGEBORG POGLAYEN-NEUWALL and I. POGLAYEN-NEUWALL

Receipt of Ms. 26. 1. 1993
Acceptance of Ms. 23. 4. 1993

The dental formula for *Bassariscus* sp., 3/3-1/1-3/4-3/2 = 40, as reported by HALL (1981) is valid for *Bassariscus astutus*. This is also evidenced by closely monitoring the tooth development of 31 young of this species (POGLAYEN-NEUWALL and POGLAYEN-NEUWALL 1993).



Upper jaw of a ♂ *Bassariscus sumichrasti,* 113 days old. Note deciduous molariform premolar 4 in the process of being replaced by molariform permanent premolar 4. (From X-ray by Dr. K. F., LYON)

Six Central American cacomixtles *(Bassariscus sumichrasti),* born in the colony of the authors, were also checked every other day for tooth eruption and succession. The dentition for this species, however, was determined to be 3/3-1/1-4/4-2/2 = 40 (figure).

References

HALL, E. R. (1981): The mammals of North America. New York: John Wiley and Sons.
POGLAYEN-NEUWALL, I.; POGLAYEN-NEUWALL, I. (1993): Behavior, reproduction, and postnatal development of *Bassariscus astutus* (Carnivora; Procyonidae). D. Zool. Garten (NF) **63**, 73–125.

Authors' address: Dr. INGEBORG POGLAYEN-NEUWALL and Dr. IVO POGLAYEN-NEUWALL, 1765 N. Indigo Drive, Tucson, AZ 85745, USA

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5805-0312 $ 02.50/0

Z. Säugetierkunde 58 (1993) 313–315

ISSN 0044-3468

The Jungle cat, *Felis chaus* Güldenstaedt, 1776, in Jordan

By D. Kock, D. M. Shafie, and Z. S. Amr

Forschungsinstitut Senckenberg, Frankfurt a. M., Germany, Yarmouk Natural History Museum, and Jordan University of Science and Technology, Irbid, Jordan

Receipt of Ms. 1. 2. 1993
Acceptance of Ms. 29. 3. 1933

The Yarmouk Natural History museum, Irbid, Jordan, exhibits a mounted female cat, which a visiting mammalogist identified as desert lynx, *Felis (Caracal) caracal* Schreber, 1776. However, upon inspection in the collection (5. V. 1992), this cat immediately distinguished itself as *Felis (Felis) chaus* Güldenstaedt, 1776 by its black markings on forelegs, black bars on dorsal side of tail and black tip of tail together with the grizzled brownish colouration. The impression of a desert lynx may have been elicitated by its physical aspect (long limbs, short tail) and a superficial similarity by tufts on tip of the ears and by blackish face marks (lacrimal stripe).

The present specimen has no character of *F. caracal* (e.g. coat cinnamon to reddish-fawn, ears outside wholly black, long pencil on tip of ears, short face), but instead has 3–4 black half-rings on dorsal side of tail, black marks inside and on back of forelimbs, underside yellowish, all typical of *F. chaus*. The blackish coloured back of ear bears an ochre bar running across, as in *chrysomelanotis* Nehring, 1902, a synonym of *F. ch. furax* De Winton (1898). The external traits of both *F. chaus* and *F. caracal* as keyed by Corbet (1978) and illustrated (e.g. Anderson 1902; Prater 1965; Dorst and Dandelot 1970; Haltenorth and Diller 1977; Kingdon 1990; Le Berre 1990) render both species easily distinguishable from each other.

The distribution in the Near East as compiled by Harrison (1968) and Harrison and Bates (1991) needs specification and completion, leaving aside vague and generalized information. Available records are (see Figure):

Lebanon: Lortet (1880); Tripolis (= 1st record).

Syria: Haver (1985); Gamla 32.54.N–35.45.E, Golan (= 1st Syrian record of the present subspecies!).

Israel: Harrison (1968): nr. Kefar Ruppin 32.27.N–35.33.E (HZM); Hazera (HZM). Ilani and Shalmon (1983): Hula valley N-3; Moshav Ami quam H-9. Anonymous (1985): SW. shore of Lake Kinneret; Jordan River Park, E. shore L. Kinneret. Chaver (1986): springs of Yarqon River. Ilani (1986): Nahal Alexander. *Anonymous* (1990): S of Kibbutz Titrat Zvi, upper Jordan valley N-10; Kibbutz Neve Eitan N-9; Zeta winter pools on coastal plain G-10.

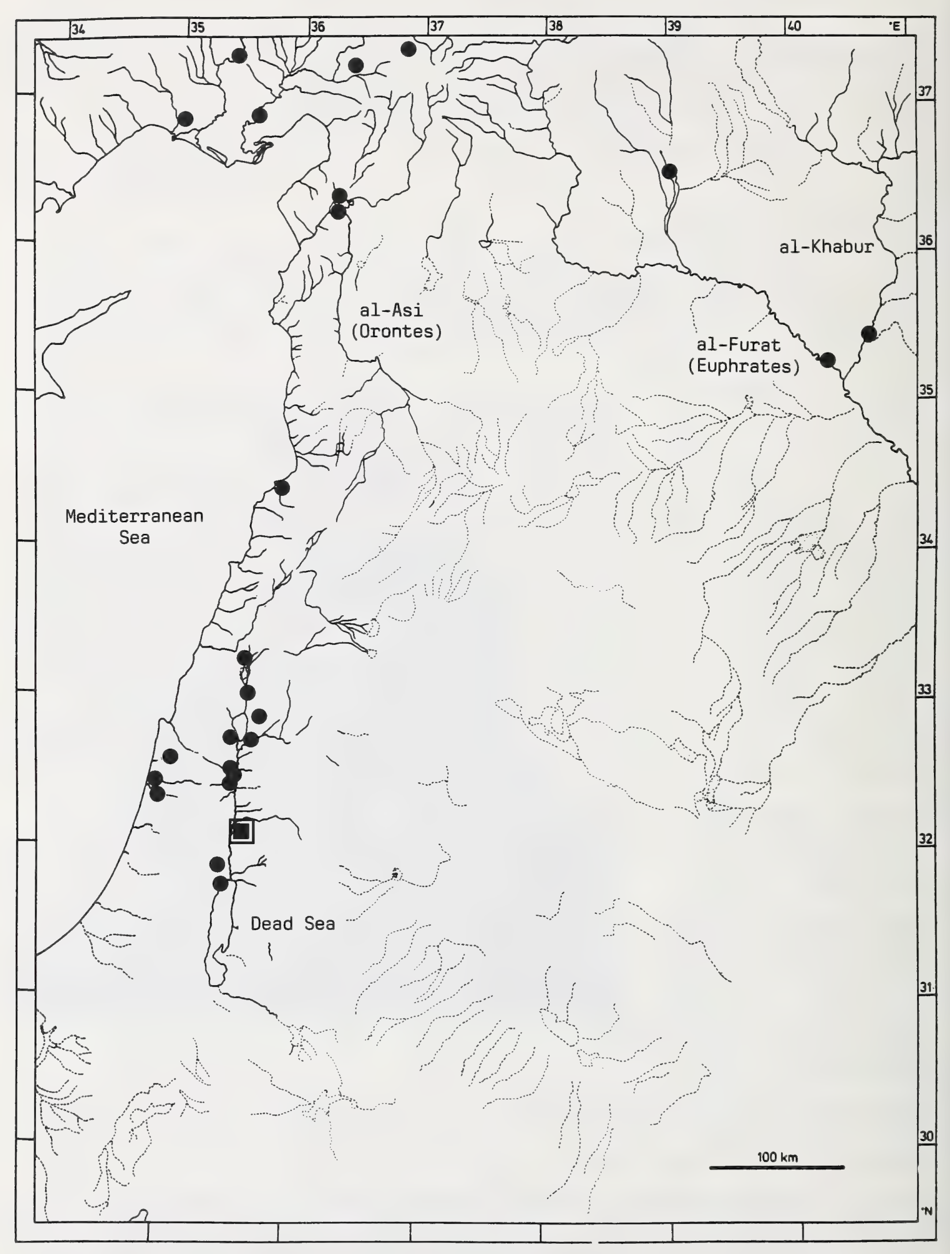
West Bank: De Winton (1898): ar-Riha (= Jericho), holotype of *F. ch. furax*. Nehring (1902a, b): lower Jordan valley, i.e. N of Dead Sea. Nehring (1902b): Ain Dscheir = Ain ed Dschuheijir, NW shore Dead Sea.

Osborn and Helmy (1980) and Kingdon (1990) mention *F. chaus* for Jordan, most probably based on the oftenly cited Jericho record (West Bank), as in Harrison (1968) and Clarke (1977). The species has not been formally recorded from Transjordan, although Nehring's (1902b) specimens could have been from either bank of the Jordan river. Thus the eventual discovery of *F. chaus* in Transjordan could be predicted. The

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5805-0313 $ 02.50/0

present specimen was collected near Damyeh Bridge (= Ed Damije) on the east bank of the Jordan River, Balqa Governorate, S of the Wadi Zerka confluence on the 9. Nov. 1988.

The skull of this specimen is not available for comparison. In view of the limited reference material available to us, we can hardly comment on its subspecific identity. This



Distribution of *Felis chaus furax* in the Levante; additional record = framed square, records (= black dots) for Turkey after KUMERLOEVE (1967), for Syria after HARRISON and BATES (1991), and unpublished data

is in contrast to CORBET (1978) who does not recognize any subspecies. The present specimen is less marked with black than *F. ch. nilotica* De Winton, 1898 as figured by ANDERSON (1902), but has the ochre band across the outside of ear similar, however not contrasted by a dark upper tip. We allocate it to *F. ch. furax* De Winton, 1898, typified by heavy dentition, because of very close geographic proximity. This subspecies is isolated from *nilotica* of the Nile valley and may be geographically separated in the Near East (Figure) from the population of Iraqi and Syrian Mesopotamia (= Gezira). The latter is intermediate in size of teeth to the nominate form (POCOCK 1951). Turkish populations (KUMERLOEVE 1967) are taxonomically unclassified.

Comparative material (skins only): *Felis chaus nilotica* De Winton, 1898: Egypt, "Lower Egypt", SMF 4221, 34667. *F. ch. affinis* Gray, 1830: Pakistan, Kashmir, SMF 44817; "Pakistan", SMF 65180. *F. ch. kutas* Pearson, 1832: India, Delhi, SMF 15727; Bangaladesh, Modhupur Jungle, Tangail Distr., SMF 61215.

Acknowledgements

D. K. sincerely thanks Prof. A. M. DISI, Department of Biology Science, University of Jordan, Amman, and both his co-authors for their hospitality in Jordan.

References

ANONYMOUS (1985): S.P.N.I. field study centers. Isr. Land and Nature **11**, 21–50.
ANDERSON, J. (1902): Mammals of Egypt: Mammalia. Revised and completed by W. E. DE WINTON. London: Hugh Rees.
— (1990): Jungle cats in groups. Isr. Land and Nature **16**, 72.
CHAVER, Y. (1986): Afeq Pass at the sources of the Yarqon River. Isr. Land and Nature **11**, 140–144.
CLARKE, J. E. (1977): A preliminary list of Jordan's mammals. Amman: Royal Soc. Conserv. Nature.
CORBET, G. B. (1978): The mammals of the Palaearctic region: a taxonomic review. London: Brit. Mus. Nat. Hist.
DE WINTON, W. E. (1898): *Felis chaus* and its allies. Ann. Mag. nat. Hist. (7) **2**, 291–294.
DORST, J.; DANDELOT, P. (1970): A field guide to the larger mammals of Africa. London: Collins.
HALTENORTH, TH.; DILLER, H. (1977): Säugetiere Afrikas und Madagaskars. München, Bern, Wien: BLV Verlagsges.
HARRISON, D. L. (1968): The mammals of Arabia. Vol. **2**. Carnivora, Artiodactyla, Hyracoidea. London: Ernest Benn.
HARRISON, D. L.; BATES, P. J. J. (1991): The mammals of Arabia. 2nd ed. Sevenoaks: Harrison Zool. Mus.
HAVER, Y. (1985): Gamla, fortress of the Golan. Isr. Land and Nature **11**, 96–99.
ILANI, G. (1986): More cats. Isr. Land and Nature **12**, 38.
ILANI, G.; SHALMON, B. (1983): Jungle cats. Isr. Land and Nature **9**, 83.
KINGDON, J. (1990): Arabian mammals. A natural history. Bahrain: Al Areen Wildl. Park and Res.
KUMERLOEVE, H. (1967): Zur Verbreitungsgeschichte kleinasiatischer Raub- und Huftiere sowie einiger Großnager. Säugetierkdl. Mitt. **15**, 337–409.
LE BERRE, M. (1990): Faune du Sahara. Vol. **2**. Mammifères. Paris: Lechevalier, R. Chabaud.
LORTET, M. (1880): Das heutige Syrien. III. Globus **38**, 129–134.
NEHRING, A. (1902a): Die geographische Verbreitung der Säugethiere in Palästina und Syrien. Mitt. und Nachr. des Palästina-Ver. **1902**, 49–63.
— (1902b): Über einen neuen Sumpfluchs (*Lyncus chrysomelanotis,* n. sp.) aus Palästina. Sitz.-Ber. Ges. naturf. Fr. Berlin **1902**, 123–128.
OSBORN, D. L.; HELMY, I. (1980): The contemporary land mammals of Egypt (including Sinai). Fieldiana Zoology (N.S.) **5**, 1–579.
POCOCK, R. I. (1951): Catalogue of the genus *Felis*. London: Brit. Mus, nat. Hist.
PRATER, S. H. (1965): The book of Indian animals. 2nd ed., Bombay: Bombay Nat. Hist. Soc., Prince Wales Mus. W. India.

Authors' addresses: Dr. DIETER KOCK, Forschungsinstitut Senckenberg, Senckenberg-Anlage 25, D-60325 Frankfurt a. M., Germany; DARWISH M. SHAFEI, Yarmouk Natural History Museum, Irbid, Jordan: Dr. ZUHAIR S. AMR, Jordan University of Science and Technology, Irbid, Jordan

Z. Säugetierkunde 58 (1993) 316–318

ISSN 0044-3468

Vertebral osteophytosis in cetacea

Spondylosis or spondylitis?

By E. J. O. Kompanje

Natuurmuseum Rotterdam, Nederlande

Receipt of Ms. 26. 10. 1992
Acceptance of Ms. 16. 4. 1993

Pathological deformations of the vertebral column in cetacea are commonly diagnosed as spondylitis deformans (Slijper 1931, 1936; Van Bree and Nijssen 1964; Cowan 1966; Van Bree and Duguy 1970; Paterson 1984; Kinze 1986). Others speak of spondylosis or ankylosing hyperostosis of the spine (Lagier 1977), ankylosing spondylosis (Martineau et al. 1988) or spondylosis deformans (Klima 1992).

Spondylosis and spondylitis are two different diseases with apparently the same appearance. A differential diagnosis is, however, often possible. The question arises whether both diseases occur in cetacea, or that one is misdiagnosed for the other.

Spondylosis deformans is also known as vertebral osteophytosis, spondylosis hyperostotica or Forestier syndrome (Leiber and Olbrich 1972; Steinbock 1976). In man, spondylosis deformans is a very common condition being present in almost all persons over sixty years of age. The initial lesion of spondylosis deformans occurs in the intervertebral disk, especially in the interior part: the nucleus pulposus. With increasing age this nucleus becomes more collagenous. The vertebrae are firmly attached along their marginal ridges by fibers from the annulus fibrosus and longitudinal ligaments. As result of degenerative tearing of the annulus fibers, the nucleus protrudes against the anterior ligaments. This protrusion provokes new bone formation, produced by the periosteum, as a result of which marginal osteophytes are formed. These osteophytes of adjoining vertebrae impinge on one another, while after fusing they produce a bony ankylosis. This impingement of osteophytes and ankylosing fusing is clearly shown in the vertebrae of the Harbour porpoise *(Phocoena phocoena)* in the figure.

Ankylosing spondylitis (spondylitis ankylopoetica) is also known as spondylitis deformans, rheumatoid spondylitis, Bechterew-Marie-Strümpell disease or fibrositis ankylopoetica (Leiber and Olbrich 1972; Steinbock 1976). In man, the disease starts in the sacro-iliac joints and spreads upward involving the synovial joints of the vertebrae and spinal ligaments. The initial lesion is a rheumatoid inflammation of the synovial (apophyseal and costoverbral) joints. Ankylosis of these joints develops during this process, often in the entire vertebral column ('Bamboo spine'). Paravertebral fusing starts, as in spondylosis deformans, in the annulus fibrosus, caused by inflammation of fibrous tissue.

Progressive cases of spondylosis may have the same appearance as ankylosing spondylitis, but in ankylosing spondylitis the bony bridge between the vertebrae occurs close to the vertebral body, contrary to the thick and irregular osteophytes in spondylosis. These fused osteophytes are situated several millimeters from the vertebral bodies.

There is an alternate use of the terms spondylitis and spondylosis throughout the zoological and veterinary literature. Hansen (1951) appeared to be the first in veterinary literature to use the term spondylosis. The lesions in cetacea present characteristics similar to the deformations caused by spondylosis in other mammalian species. It is striking that the disease is common in man and other mammals moving in upright position, as well as in

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5805-0316 $ 02.50/0



Impingement of osteophytes and ankylosing fusing in vertebrae of *Phocoena phocoena*

Cetacea. Due to man's anatomy, the intervertebral discs are subject to constant strain for which they were not originally designed. As a result of this, degeneration commonly occurs with increasing age. Cetacea use their vertebral column, especially the lumbal and caudal vertebrae, for locomotion. The similarity between man and other mammals living upright lies in the overload of the vertebral column. KLIMA (1992) mentioned the same analogy between man and Cetacea. This could be the answer to the problem in the latter, but does not solve the question regarding the cause of this disease in quadrupedal mammals.

Changes within the annulus fibrosus appears to play a major part in the development of vertebral osteophytes. Changes occurring within the ventral annulus fibrosus seem to be degenerative. Stresses on the outer annular lamellae seem to cause avulsions of their attachments, after which formation of the osteophyte occurs in fibrous tissue on the outside of the annulus fibrosus. The development of osteophytes on the marginal ridges of the vertebrae is a slow, non-inflammatory process. Use of the term spondylitis is without justification since inflammation takes no part in the pathogenesis.

Concluding, spondylosis deformans or vertebral osteophytosis is the term to be used for this disease in Cetacea. It seems evident that this phenomenon has little to do with inadequat feeding conditions, often offered as an explanation for this disease (HOUS-

semayne du Boulay 1976; Kinze 1986). Spondylosis in man is very common, even in 'well-fed' communities (Bourke 1967).

References

Bourke, J. B. (1967): A review of the paleopathology of the arthritic diseases. In: Diseases in antiquity. Ed. by D. Brothwell and A. T. Sandison. Springfield: Charles C. Thomas. Pp. 352–370.

Bree, P. J. H. van; Duguy, R. (1970): Sur quelques aberrations pathologiques chez les petits Cétacés. Zool. Garten **39**, 11–15.

Bree, P. J. H. van; Nijssen, H. (1964): On three specimens of *Lagenorhynchus albirostris* Gray, 1846 (Mammalia, Cetacea). Beaufortia **11**, 85–93.

Cowan, D. F. (1966): Pathology of the pilot whale. Arch. Path. **82**, 178–189.

Hansen, H. J. (1951): A pathologic-anatomical interpretation of disc degeneration in dogs. Acta orthop. scand. **20**, 280.

Houssemayne du Boulay, E. P. G. (1976): Nutritional bone diseases as a predisposing factor in spondylosis in primates. J. Anat. **122**, 196.

Kinze, C. Chr. (1986): Note on the occurrence of Spondylitis deformans in a sample of harbour porpoises *(Phocoena phocoena)* taken in Danish waters. Aquatic Mammals **12**, 25–27.

Klima, M. (1992): Spondylosis deformans der Wirbelsäule bei den Walen und beim Menschen – die gleiche Ursache? Z. Säugetierkunde, Sonderheft zu **57**, 34–35.

Lagier, R. (1977): Spondylosis in the whale- and anatomicoradiological study of an osteophyte. Scand. J. Rheumat. **6**, 245–249.

Leiber, B.; Olbrich, G. (1972): Die klinischen Syndrome. München: Urban und Schwarzenberg.

Martineau, D.; Lagacé, A.; Béland, P.; Higgins, R.; Armstrong, D.; Shugart, L. R. (1988): Pathology of stranded Beluga whales *(Delphinapterus leucas)* from the St. Lawrence Estuary, Québec, Canada J. Comp. Path. **98**, 287–311.

Authors' address: Erwin J. O. Kompanje, Museum of Natural History, P.O. Box 23452, NL-3001 KL Rotterdam, The Netherlands

KRAUSE, W. J.; CUTTS, J. H.: **Development of the Digestive System in the North American Opossum (*Didelphis virginiana*).** Advances in Anatomy, Embryology and Cell Biology Vol. 125. Berlin, Heidelberg, New York: Springer-Verlag 1992. VIII + 151 pp., 45 ill., 68 tabls. Softcover DM 115,–. ISBN 3-540-55149-2

According to the authors "*Didelphis* . . . appears to be an ideal mammalian model in which to study changes in the digestive system due to aging." This treatise "presents a summary of the published data concerning the development of the digestive system of the North American opossum, *Didelphis virginiana*". The authors compile very valuable data concerning the prenatal and postnatal development of the oral cavity, esophagus, stomach, small and large intestines, pancreas and liver. Their text is based on an extensive list of references that requires 18 pages, but covers almost exclusively the histological, and especially the cytological develoment of the digestive system.

The selection of data presented appears to be quite random. The topographical changes of the different digestive organs during ontogenetic development are not described. Quantitative changes are indicated by tables listing the weights of the respective organ walls at different ages, but embryological reconstructions or models that illustrate the development of selected parts of the gastrointestinal tract of *Didelphis virginiana* are not presented, in fact, not even mentioned. In some cases the terminology applied is not in accordance with the latest version of the Nomina Anatomica and Nomina Histologica. Some examples for the almost haphazard presentation of data and non-technical terminology are:

1. The development of the submandibular salivary glands has been examined in detail and is presented on more than nine pages, including three tables and seven electron micrographs that demonstrate cytological details. Although the reader will accept that not all details of the opossum's digestive system have been investigated to date, it is difficult to understand why no information is given on the other types of salivary glands that can be found in the opossum (greater and lesser sublingual, parotid, and molar glands).
2. It is not clear why ten tables were devoted to the development of immunoreactive cells in the "intestinal tract" of the opossum, but no explanation is given why in these tables the authors make a differentiation between "duodenum" and "small intestine". In the anatomical literature the duodenum is considered as the first part of the small intestine.
3. The term "Muscularis externa" must be considered as non-technical nomenclature and should be replaced by "Tunica muscularis".
4. As an important period of the young opossum's life, weaning is mentioned quite often in the discussion of the histological ontogeny of the gastrointestinal system. However, it is not mentioned before page 124 (!) that weaning takes place about 74 days post partum; three pages later the reader is informed that the "opossum and other marsupials rely on the mother's milk for a long period (approximately 90 days in the opossum) . . ." No explanation for this discrepancy is given.

In general, this publication presents a wealth of valuable data on an interesting marsupial that can be considered as a model for medical research, but the mammalogical aspects of the ontogeny of the digestive system are not considered in sufficient detail.

P. LANGER, Giessen

NICKEL, R.; SCHUMMER, A.; SEIFERLE, E.: **Lehrbuch der Anatomie der Haustiere.** Bd. IV: Nervensystem, Sinnesorgane, Endokrine Drüsen. 3. völlig neubearb. Aufl. Berlin und Hamburg: Paul Parey 1992. 564 S., 265 Abb. DM 198,–. ISBN 3-489-58216-0

Der 4. Band dieses bedeutenden und wichtigen 5bändigen Lehrbuchs der Veterinär-Anatomie ist nun, acht Jahre nach der letzten, in einer 3. Aufl. neubearbeitet erschienen. Einziger Autor dieses umfassenden Bandes ist G. BÖHME, Veterinär-Anatom an der Freien Universität Berlin. Der Band behandelt die Steuerungssysteme der klassischen Haussäugetiere aus allgemeiner sowie gruppen- und artspezifischer Sicht. Der deutlich größte Anteil ist wiederum dem Nervensystem gewidmet (384 S.). Es wird in den Kapiteln Allgemeines, Zentralnervensystem, peripheres Nervensystem abgehandelt. Die Kapitel über Sinnesorgane (86 S. sehr ausführlich Auge und Stato-akustisches Organ) und endokrine Drüsen (28 S. Hypophyse, Schilddrüse, Epithelkörperchen, Nebenniere, Paraganglien, Epiphyse) fallen entsprechend kürzer aus. In der für dieses Lehrbuch kennzeichnenden Weise sind die klaren topographischen Beschreibungen durch beeindruckende z. T. farbige Abbildungen illustriert, und über die anatomischen Schilderungen hinaus werden funktionelle Zusammenhänge stets hervorgehoben. Diese Neubearbeitung zeigt deutlich einige Modernisierungen, die sich auch im Literaturverzeichnis niederschlagen.

Das Buch ist zwar für Veterinär-Mediziner konzipiert und stellt in dieser Hinsicht eine beeindrukkende Kompilation dar, es kann aber auch für interessierte Säugetierkundler von Nutzen sein. Aus stammesgeschichtlicher und zoologischer Sicht muß allerdings über einige Mängel hinweggesehen werden, insbesondere im Hinblick auf die evolutive Entfaltung und adaptive Radiation von Säugetiergehirnen. Der gut fundierte Wissensstand auf diesem Gebiet wird wenig berücksichtigt, und manche älteren Lehrmeinungen wurden nicht revidiert. Hirnteilzuordnungen und -gliederungen entsprechen nicht immer vergleichend neuroanatomischen Gepflogenheiten. Ferner sind einige Abbildungen zu klein, unübersichtlich und wenig informativ, und Formulierungen wie „Säugetierreihe“ oder „Wirbeltierreihe“ wirken störend.

D. KRUSKA, Kiel

PETZSCH, H.: **Urania Tierreich, Säugetiere.** Bearb. von R. PIECHOCK. Leipzig, Jena, Berlin: Urania-Verlag 1992. 559 S., zahlr. farb. Abb. DM 88,–. ISBN 3-332-00499-9

Der erste Eindruck der neuen Auflage des Säugetierbandes dieser „großen farbigen Enzyklopädie“ ist sehr positiv: Seine bestechend schönen und durchgehend farbigen Photos geben eine gute Vorstellung vom Habitus der besprochenen Säugetiere. Eine genauere Lektüre bereitet allerdings beträchtliche Enttäuschungen. Als erstes fällt auf, daß die Systematik modernen Vorstellungen nicht entspricht: So sollen die Tupaiidae eine Familie der Lemuriformes, also Primaten, sein. Die Ordnungen der Lagomorpha und der Rodentia sind zur Kohorte der Glires – Nager, die Hyracoidea oder Schlieftiere (sic!) mit den Proboscidea und Sirenia zur Überordnung der Paenungulata zusammengefaßt. Als abschließendes Beispiel sei aufgeführt, daß zur Familie der Tayassuidae nach dem vorliegendem Band „nur die Gattung *Tayassu* mit zwei Arten“ gehören soll, *Catagonus wagneri* hingegen wird nicht erwähnt.

Ein Vergleich der 1. Auflage 1966 des von HANS PETZSCH verfaßten Säugetierbandes vom ‚Urania Tierreich‘ mit der 1. Auflage 1992 (sic!) der nach dem Tode des Erstautors von RUDOLF PIECHOCKI bearbeiteten Fassung des gleichen Werkes, erweckt den Eindruck, daß die Säugetierkunde ein Zweig der Zoologie ist, in dem in den vergangenen 26 Jahren nur ein sehr geringer Wissenszuwachs zu verzeichnen war. Über weite Abschnitte ist der Text völlig unverändert aus der alten Auflage übernommen worden. Die Bearbeitungen beschränken sich meist auf nur wenige Zeilen umfassende Ergänzungen oder Kürzungen. Der Text auf dem Schutzumschlag behauptet hingegen, daß „der Stoff wissenschaftlich auf den neuesten Stand gebracht“ worden sei. Bei paralleler Lektüre beider Auflagen blieben umfangreiche und entscheidende Neubearbeitungen verborgen!

Daten zur Körpergröße, Ökologie oder Biologie der besprochenen Säugetiere sind in den Text eingearbeitet und damit für den interessierten Leser schwer auffindbar; tabellarische Zusammenstellungen oder Graphiken findet man nicht. Beim Vergleich fällt sogar auf, daß in der Auflage von 1992 Zahnformeln, welche vor 26 Jahren noch geboten wurden, eliminiert worden sind!

Wenn auf dem Schutzumschlag des hier besprochenen Bandes behauptet wird, daß das Urania Tierreich „für Studenten und Lehrer biologischer Fachrichtungen unentbehrlich“ sei, so muß dem entgegengehalten werden, daß für diesen Leserkreis die gebotenen Informationen nicht aktuell genug sind. Der Text läßt die neueren Entwicklungen in der Mammalogie weitgehend unberücksichtigt. Bei Landsäugetieren bietet der Text häufig alte, historisch durchaus interessante Zoobeobachtungen. Damit wird auf die Leserschaft verwiesen, welche sich von dem vorliegenden Band angesprochen fühlen könnte: „Tierliebe“ findet bei Stadtmenschen oft nur ihre Erfüllung bei Zoobesuchen. Das vorliegende Werk kann vom interessierten Laien als „Begleit- und Nachbereitungs-Buch“ für den Zoobesuch genutzt werden.

Die Schilderung eines erfreulichen Befundes schließe diese Besprechung ab: Im Abschnitt über den Elbebiber (*Castor fiber albicus*), um dessen Erforschung und Schutz sich der Bearbeiter dieses Buches große Verdienste erworben hat, heißt es in der Auflage von 1966, daß Ende 1961 nur 210 Elbebiber in freier Wildbahn existierten. 1992 hingegen wird berichtet, daß 1988 in über 1000 Revieren annähernd 2380 Individuen festgestellt werden konnten!

P. LANGER, Gießen

Erscheinungsweise und Bezugspreis 1993: 6 Hefte bilden einen Band. Jahresabonnement Inland: DM 378,– zuzüglich DM 13,80 Versandkosten; Jahresabonnement Österreich: öS 2940,– zuzüglich öS 140,– Versandkosten; Jahresabonnement Schweiz: sfr 364,– zuzüglich sfr 17,50 Versandkosten; Jahresabonnement EG-Binnenmarkt-Länder mit USt-ID-Nr.: DM 354,– zuzüglich DM 16,82 Versandkosten; Jahresabonnement EG-Binnenmarkt-Länder ohne USt-ID-Nr. und Drittländer: DM 378,– zuzüglich DM 18,– Versandkosten. Das Abonnement wird zum Jahresanfang berechnet und zur Zahlung fällig. Es verlängert sich stillschweigend, wenn nicht spätestens am 15. November eine Abbestellung im Verlag vorliegt. Die Zeitschrift kann bei jeder Buchhandlung oder bei der Verlagsbuchhandlung Paul Parey GmbH & Co. KG, Spitalerstraße 12, W-20095 Hamburg, Bundesrepublik Deutschland, bestellt werden. Die Mitglieder der „Deutschen Gesellschaft für Säugetierkunde“ erhalten die Zeitschrift unberechnet im Rahmen des Mitgliedsbeitrages.

Z. Säugetierkunde 58 (1993) 5, 257–320

Einem Teil der Auflage liegt der Bericht 1992 des Schatzmeisters der DGS bei

6), 321–384, Dezember 1993 ISSN 0044-3468 C 21274 F

ZEITSCHRIFT FÜR SÄUGETIERKUNDE

INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Organ der Deutschen Gesellschaft für Säugetierkunde



Verlag Paul Parey Hamburg und Berlin

This journal is covered by Biosciences Information Service of Biological Abstracts, and by Current Contents (Series Agriculture, Biology, and Environmental Sciences) of Institute for Scientific Information

---

Die Zeitschrift für Säugetierkunde veröffentlicht Originalarbeiten und wissenschaftliche Kurzmitteilungen aus dem Gesamtgebiet der Säugetierkunde, Besprechungen der wichtigsten internationalen Literatur sowie die Bekanntmachungen der Deutschen Gesellschaft für Säugetierkunde. Verantwortlicher Schriftleiter im Sinne des Hamburgischen Pressegesetzes ist Prof. Dr. Dieter Kruska.

Zusätzlich erscheint einmal im Jahr ein Heft mit den Abstracts der Vorträge, die auf der jeweiligen Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde gehalten werden. Sie werden als Supplement dem betreffenden Jahrgang der Zeitschrift zugeordnet. Verantwortlich für ihren Inhalt sind ausschließlich die Autoren der Abstracts.

Manuskripte: Manuskriptsendungen sind zu richten an die Schriftleitung, z. Hd. Prof. Dr. Dieter Kruska, Institut für Haustierkunde, Biologiezentrum der Christian-Albrechts-Universität, Am Botanischen Garten 9, D-24118 Kiel, Bundesrepublik Deutschland. Für die Publikation vorgesehene Manuskripte sollen gemäß den „Redaktionellen Richtlinien" abgefaßt werden. In ihnen finden sich weitere Hinweise zur Annahme von Manuskripten, Bedingungen für die Veröffentlichung und die Drucklegung, ferner Richtlinien für die Abfassung eines Abstracts und eine Korrekturzeichentabelle. Die Richtlinien sind auf Anfrage bei der Schriftleitung und dem Verlag erhältlich.

Sonderdrucke: Anstelle einer Unkostenvergütung erhalten die Verfasser von Originalbeiträgen und Wissenschaftlichen Kurzmitteilungen 50 unberechnete Sonderdrucke. Mehrbedarf steht gegen Berechnung zur Verfügung, jedoch muß die Bestellung spätestens mit der Rücksendung der Korrekturfahnen erfolgen.

Fortsetzung 3. Umschlagseite

 Verlag: Paul Parey GmbH & Co. KG, Hamburg und Berlin. Anschriften: Spitalerstr. 12, D-20095 Hamburg; Seelbuschring 9–17, D-12105 Berlin, Bundesrepublik Deutschland. – Printed in Germany by Westholsteinische Verlagsdruckerei Boyens & Co., Heide/Holst.

Z. Säugetierkunde 58 (1993) 321–329

ISSN 0044-3468

Effects of denervation on palmar sweating in the Rhesus monkey (*Macaca mulatta*)

By A. A. Smith

School of Podiatric Medicine, Barry University, Miami Shores, Florida, USA

Receipt of Ms. 16. 6. 1992
Acceptance of Ms. 29. 4. 1993

Abstract

Observed the effects of denervation on the response of eccrine sweat glands to exogenous methacholine. Interprets these results in the light of recent studies of sweating.

Cutting the nerve supply to the eccrine sweat glands of 3 female rhesus monkeys ended spontaneous production of visible sweat. Within 2 weeks the sweat glands' capacity to produce visible sweat in response to sudorific drugs is also lost. The nerves visibly degenerate over a 1 month period. These effects are like the effects of cutting the nerve supply to human eccrine sweat glands.

The denervated sweat glands remained histologically normal throughout the 5 weeks of observation. They also continued to show phosphorylase a activity, which is normally associated with sweat production. This suggests that denervated sweat glands produce water vapor. Other studies of monkey and human sweat glands provide further evidence of vapor sweating in both denervated and normal sweat glands.

Vapor sweating is an efficient cooling mechanism for a furry animal. The spread of eccrine sweat glands from the palms and soles to the general body surface over the course of the evolution of higher primates was due to the survival value of vapor sweating.

Introduction

Most mammals have eccrine sweat glands, which secrete clear, odorless sweat, only on the palms and soles (Kuno 1956; Montagna and Parakkal 1959). Like man, the apes and monkeys of the Old World (Montagna and Yun 1962; Montagna et al. 1964; Machida et al. 1964) and the higher New World monkeys (Perkins and Machida 1967; Machida and Giacometti 1968) also have eccrine sweat glands on the general body surface.

Eccrine sweat glands are normally under the control of cholinergic nerves (Dale and Feldberg 1934), although they also have some adrenergic innervation (Uno and Montagna 1975).

The eccrine sweat glands on the soles of cats (Nakamura and Hatanaka 1958) and lemurs (Sakurai and Montagna 1965) still respond to injected acetylcholine after the nerve supply is severed. Human eccrine sweat glands, even those on the palms and soles, require an intact nerve supply to produce visible sweat in response to sudorific drugs (Coon and Rothman 1941; Silver et al. 1963). The sweat glands of the African green monkey, *Cercopithecus aethiops*, also become unresponsive after denervation (Sakurai and Montagna 1964).

This study was undertaken in hope that histochemical observations on the glands after denervation would help to elucidate the mechanism of the loss of responsiveness. Several recent studies show that this data also suggests how thermoregulatory sweat glands could have evolved in furry animals.

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5806-0321 $ 02.50/0

Material and methods

Three female rhesus monkeys, *Macaca mulatta*, were used in this study. The median, ulnar, and radial nerves in one upper arm of each monkey were severed (and sutured to allow regeneration after the experiment) under phencylclidine anesthesia.

The palm and fingertips of the operated hands were tested for spontaneous sweating before and after the operation by pressing bromphenol blue paper (Sakurai and Montagna 1964) against them. At the same time a different fingertip or palmar pad on the denervated hand of each monkey was injected with 20 μg acetyl-β-methylcholine chloride in 50 μl saline to test the sweat glands' capacity to sweat. Liquid sweat was visualized by pressing bromphenol blue paper against the injected area. Similar observations were made on the unoperated palms.

Biopsies were taken (under phencyclidine anesthesia) from the denervated palms immediately before the nerves were cut and at irregular intervals thereafter. A quarter of each biopsy was fixed in Helly's fluid, dehydragyrified in Lugol's iodine, embedded in Paraplast, sectioned at 7 μm, and stained with the PAS technique followed by hematoxylin (Lillie 1954).

A second quarter of each biopsy was frozen in liquid nitrogen, sectioned in a cryostat at 20 μm, and incubated in the medium of Eränkö and Palkama (1961) without adenylic acid to show phosphorylase a activity. Staining was preserved by mounting in iodized "Histoclad" (Smith et al. 1966).

Frozen sections were also incubated in the medium of Burstone (1961) to show cytochrome oxidase activity. The rest of the biopsy was fixed for 1½ hours in 10 % formalin at 4 °C, sectioned at 40 μm, and incubated 5 hours in a solution of cupric sulfate and acetylthiocholine iodide to show cholinesterase activity (Gomori 1952). Some of these sections were counterstained with hematoxylin.

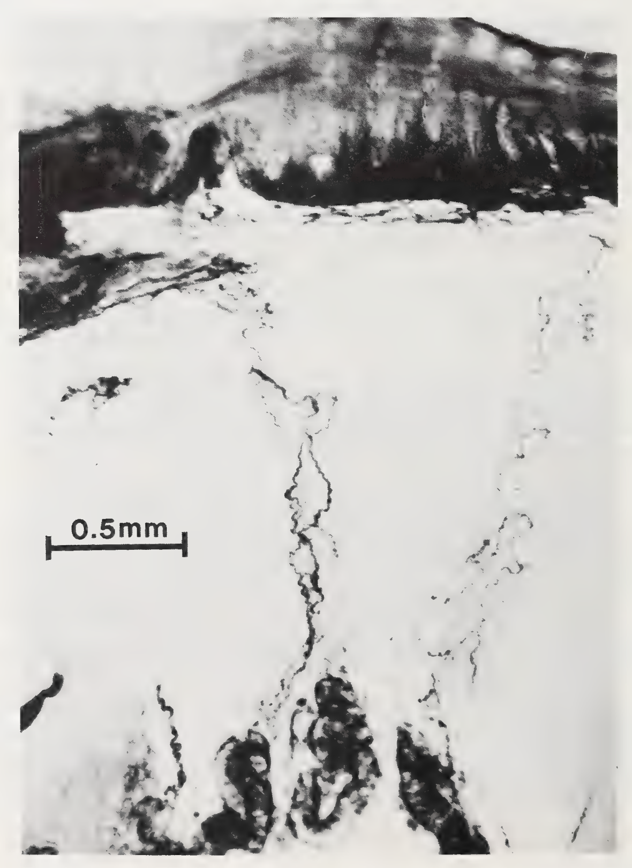


Fig. 1. Cholinergic nerves around sweat glands and their connections with the subpapillary plexus. Acetylthiocholine iodide – $CuSO_4$. ×40

Surgery and post-operative care were in conformity with the U.S. Animal Welfare Act of 1966. For a few months after the surgery, the animals required care like that given to a human with similar nerve lesions due to a misused touniquet. Although such experiments were common at the time of this work, I would not repeat this experiment today.

Results

The palms of two monkeys were sweating spontaneously before the operation. None of the operated palms sweated spontaneously immediately after denervation. Spontaneous sweating reappeared in two of the operated palms during the first week after denervation. Spontaneous sweating was never seen in a denervated palm after the end of the first week.

All 3 unoperated (control) palms sweated spontaneously after the operation.

All of the denervated palms continued to sweat in response to acetyl-β-methylcholine for the first week after denervation. During the second week all of the denervated palms ceased to respond. The control palms always responded.

Cholinesterase-positive nerve fibers surrounded the secretory coils of the eccrine sweat glands. Almost all of the fibers were circular rather than longitudinal and lay in a single surface of revolution just outside the fibroelastic capsule of the gland. A few unoriented

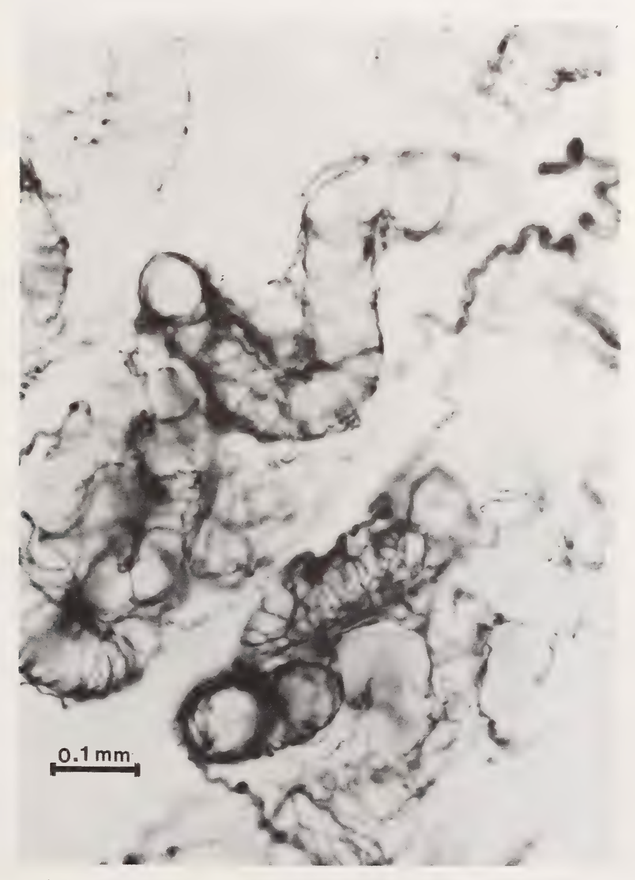


Fig. 2. Three days after denervation the cholinergic nerves around the secretory coil show no visible change. Acetylthiocholine iodide – $CuSO_4$. ×130

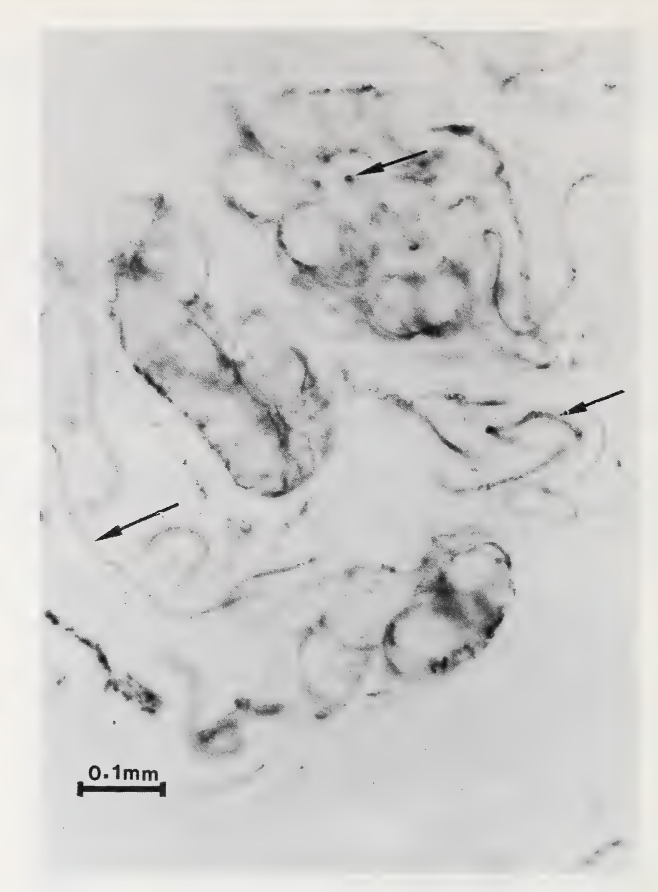


Fig. 3. Two weeks after denervation the nerves have lost most of their cholinesterase activity. Some of the enzyme lost from the nerves has collected in sweat ducts (arrows). Acetylthiocholine iodide – $CuSO_4$. ×130

nerve fibers were associated with the proximal (coiled) duct. The nerve fibers were connected with the subpapillary nerve plexus of the upper dermis (Fig. 1).

The cholinesterase-positive nerves looked completely normal for the first 3 days after denervation (Fig. 2). Acetylcholinesterase activity started to weaken after the third day after denervation and was gone by the 35th day (Fig. 3).

The eccrine sweat glands themselves remained histologically normal throughout the period of observation. There was a dramatic increase in glycogen (as shown by PAS) in the coiled ducts of the sweat glands in all 3 monkeys after denervation. Two of the monkeys had low glycogen levels in the clear cells of the secretory coils of their palmar sweat glands before denervation. All of the monkeys had high glycogen levels in their clear cells after denervation.

Moderate phosphorylase a activity was seen in the clear cells of the secretory coils both before (Fig. 4) and after (Fig. 5) denervation. Phosphorylase a activity in the coiled ducts varied more within a single skin sample than it did from one sample to another.

Cytochrome oxidase activity was high in the clear cells of the secretory coil and in all cells of the coiled duct both before and after denervation.

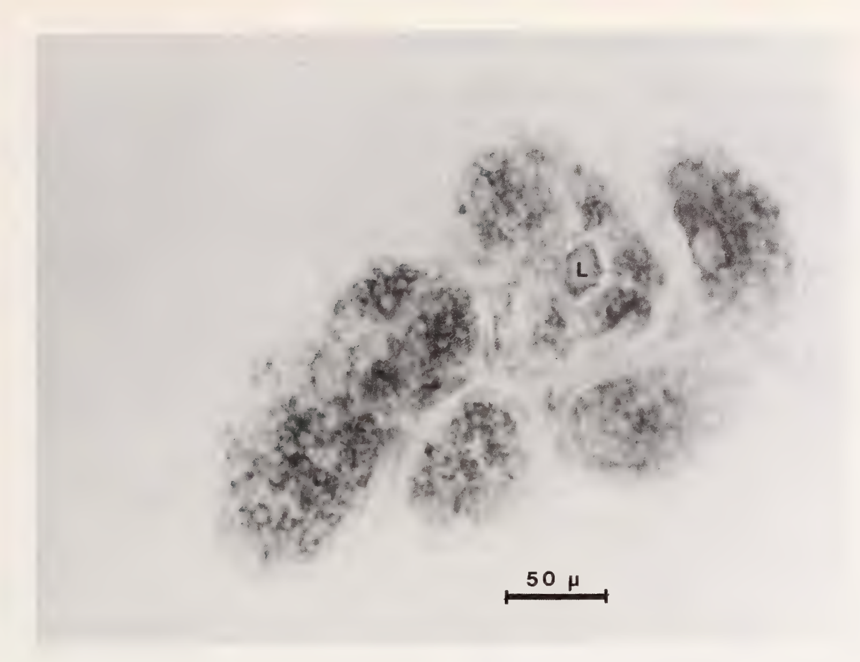


Fig. 4. Phosphorylase a activity in the secretory coil before denervation. Reaction in lumen (L) is a diffusion artefact. Iodine stain. ×280

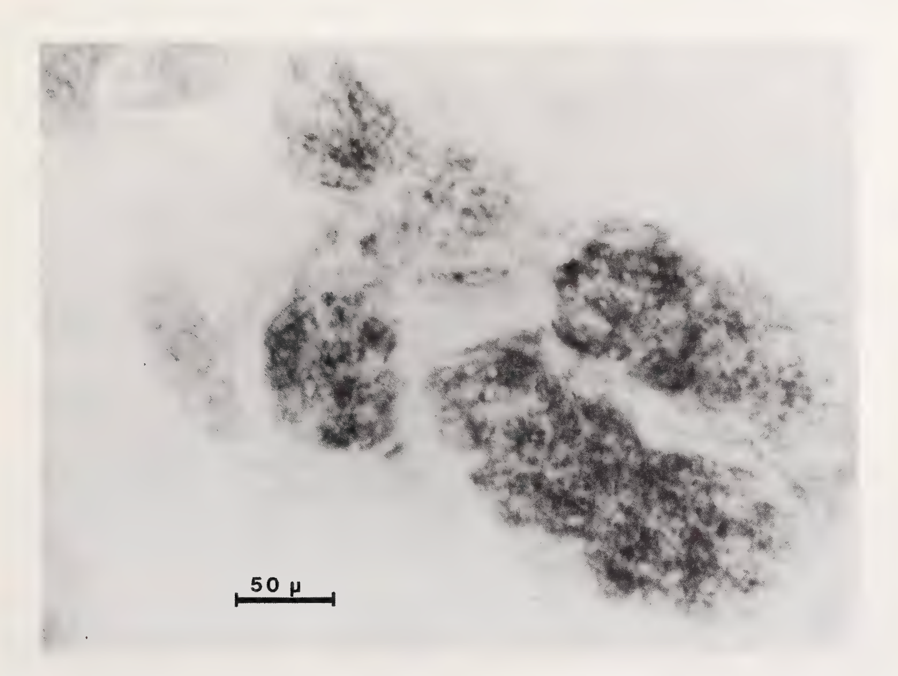


Fig. 5. Phosphorylase a activity in the secretory coil two weeks after denervation. Iodine stain. ×280

Discussion

These results show that the sweat glands of the rhesus monkey slowly lose their capacity to produce visible sweat after denervation. In this, they resemble the sweat glands of man (Coon and Rothman 1941) and the African green monkey (*Cercopithecus aethiops*) (Sakurai and Montagna 1964). The fact that this requires more than a week suggests that the process is one of acclimatization.

The production capacity of the eccrine sweat glands of the patas monkey (*Erythrocebus patas*) increseses in hot weather and decreases in cold weather (Gisolfi et al. 1985). The production capacity of human eccrine sweat glands increases after a week of the increased demand of hot weather or hard exercise (Davies 1981; Taylor 1986) and decreases when cool weather decreases demand (Torii et al. 1991).

It should be expected that the production capacity of sweat glands would decrease in response to the sharply decreased demand following denervation. Acclimatization has been found only in animals that have eccrine sweat glands on the general body surface (Coon and Rothman 1941; Sakurai and Montagna 1964; Gisolfi et al. 1985). Acclimatization is adaptive in a heat dispersal mechanism that may face different challenges over the seasons and over the life cycle.

Animals with eccrine sweat glands only on the palms and soles show denervation hypersensitivity (Nakamura and Hatanaka 1958; Sakurai and Montagna 1965). Denervation hypersensitivity increases sweat production in response to pharmacologic stimuli. Denervation hypersensitivity can be seen only if acclimatization does not occur.

Despite their loss of capacity to produce visible sweat, the denervated sweat glands of the rhesus monkey remained histologically normal. Denervated sweat glands also remain histologically normal in man (Silver et al. 1964) and the African green monkey (Sakurai and Montagna 1964). Congenitally aneural eccrine sweat glands are also histologically normal in man (Rafel et al. 1930; Swanson 1963).

The denervated sweat glands in this study also continued to show moderate levels of phosphorylase a activity, whose presence is concomitant with sweating (Smith and Dobson 1966).

Are denervated sweat glands truly devoid of function? Sympathectomized human patients, who cannot produce visible sweat, produce moist patches where one area of dry skin is held firmly against another (Hyndman and Wolkin 1941). Sweat vaporizing in the secretory coil or in the duct would be invisible and would not stain bromphenol blue paper during the customary one minute exposure, but it would condense on epidermis occluding the duct orifice.

The release of water vapor from the sweat glands would explain why humans with anhydrotic sensory neuropathy, who have aneural sweat glands, suffer less in hot weather than humans with anhidrotic ectodermal dysplasia, who have no sweat glands at all (Bowen 1957; Swanson 1963; Pinsky and DiGeorge 1966). Vapor leaving the duct cools the body just as well as sweat evaporating from the skin surface. Even vapor condensing in the duct transfers heat to the epidermis, increasing radiative and convective cooling from its surface (Thiele et al. 1972; Reay and Thiele 1977).

Vapor sweating allows an animal with thick fur to cool itself efficiently. Thus, the possession of sweat glands on the general body surface is adaptive for a mammal that is diurnally active in hot weather. Thermoregulatory eccrine sweat glands have evolved in Scandentia (Montagna et al. 1962) and among the Primates, both of which are diurnal and primarily tropical.

The absence of eccrine sweat glands from the general body surface of the diurnal lemurs (Sokolov 1982) and marmosets (Perkins 1966; Perkins 1968) suggests that the presence of eccrine sweat glands on the general body surface is not a primitive feature of primates. Although tree shrews have eccrine sweat glands on the general body surface (Montagna et

al. 1962), it is now generally agreed that the tree shrews are not primates (Van Valen 1965; Dene et al. 1966; Martin 1982).

The higher New World monkeys are diurnal and have eccrine sweat glands on the general body surface (Machida et al. 1967; Perkins and Machida 1967). Since marmosets and the other monkeys of the New World have a common ancestor that is not shared with the Old World monkeys, the extension of eccrine sweat glands to the general body surface must have evolved after the divergence of Old and New World primates (Perkins 1968; Machida et al. 1967). The absence of eccrine sweat glands from the skin of the tarsier which shares a common ancestor with the Old World monkeys tends to confirm this (Montagna and Machida 1966).

The presence of eccrine sweat glands on the general body surface of Scandentia, Cebidae, and Old World monkeys and apes is a result of parallel evolution (Montagna and Parakkal 1974; Folk and Semken 1991). The repeated evolution of thermoregulatory eccrine sweat glands is due to the survival value of vapor sweating.

Denervated sweat glands probably produce water vapor under the influence of circulating epinephrine. Although atropine prevents the appearance of liquid sweat detectable by the starch-iodine test or bromphenol blue paper, it does not prevent the delivery of water vapor to a sudorimeter (Wolf and Maibach 1974). Although some of the sudorimotor nerves secrete norepinephrine (Uno and Montagna 1975), the eccrine sweat glands have more β receptors than α receptors and are more sensitive to epinephrine (Sato and Sato 1981). Physiological levels of circulating epinephrine increase evaporative heat loss in the intact stumptail macaque, *Macaca speciosa* (Robertshaw et al. 1973). Higher levels of epinephrine can elicit visible sweat in man (Wada 1950; Chalmers and Keele 1951).

In 1935 Ogata found that some human sweat glands failed to produce liquid sweat under any stimulus (Kuno 1956). This suggests that many innervated sweat glands produce only vapor. The excess of sweat glands in histological counts in man (Montagna and Parakkal 1974) and rhesus monkeys (Smith 1969) over counts of sweat droplets on the skin of man (Montagna and Parakkal 1974) and rhesus monkeys (Johnson and Elizondo 1974) leads to the same conclusion.

Denervated sweat glands remain histologically normal because they continue to produce water vapor, which is part of the normal function of sweat glands.

Acknowledgements

The experimental part of this work was done in 1969 at the Oregon Regional Primate Research Center with support from grants FR 00163 and AM 05512 from the National Institutes of Health and grant 5T01GM00445-09 from the US Public Health Service.

The author thanks Dr. William Montagna for his advice and encouragement, Dr. Clarence Dennoy for his expert surgery, and John Ochsner of the Oregon Regional Primate Research Center for his special efforts in the care of the research animals. He also thanks Pia York of Barry University for her editorial assistance.

Zusammenfassung

Auswirkungen von Denervierung der Schweißdrüsen bei Rhesusaffen, Macaca mulatta

Die Schweißdrüsen des Rhesusaffen sind umgeben von cholinergen Nerven, die vom subpapillaren Plexus stammen. Nach Durchtrennung der Nerven von Schweißdrüsen bildet sich kein Schweiß mehr. Während der nächsten zwei Wochen verliert die Schweißdrüse ihre Fähigkeit auf Arzneien zu reagieren. Im Laufe eines Monats werden die Nerven degeneriert. Nach Durchtrennung der Nerven von menschlichen Schweißdrüsen ergeben sich ähnliche Effekte.

Die denervierte Schweißdrüse bleibt histologisch jedoch unverändert. Zusätzlich ist auch eine Aktivität der Phorphorylase a zu beobachten, die normal mit der Schweißproduktion verbunden ist. Das deutet an, daß die denervierten Schweißdrüsen Wasserdunst produzieren. Andere Studien an Schweißdrüsen von Affen und Menschen beweisen, daß denervierte und normale Schweißdrüsen Wasserdunst absondern.

Die Schweißabsonderung bei Säugetieren mit Fell hat einen kühlenden Effekt. Das Ausbreiten der

Schweißdrüsen von Handfläche und Sohle zur Oberfläche des Körpers begünstigte sehr wahrscheinlich die evolutive Radiation der höheren Affen.

Literature

Bowen, R. (1957): Hereditary ectodermal dysplasia of the anhidrotic type. South. Med. J. **50**, 1018–1021.

Burstone, M. S. (1961): Modifications of histochemical techniques for demonstration of cytochrome oxidase. J. Histochem. Cytochem. **9**, 59–65.

Chalmers, T. M.; Keele, C. A. (1951): Physiological significance of the sweat response to adrenaline in man. J. Physiol. (Lond.) **114**, 510–514.

Coon, J. M.; Rothman, S. (1941): Sweat response to drugs with nicotine-like action. J. Pharmacol. Exper. Ther. **73**, 1–11.

Dale, H. H.; Feldberg, W. (1934): The chemical transmission of secretory impulses to the sweat glands of the cat. J. Physiol. (Lond) **82**, 121–128.

Davies, C. T. M. (1981): Effect of acclimatization to heat on the regulation of sweating during moderate and severe exercise. J. Appl. Physiol. **50**, 741–746.

Dene, H. T.; Goodman, M.; Prychodko, W. (1976): Immunodiffusion evidence on the phylogeny of the primates. In: Molecular anthropology. Ed. by M. Goodman, R. E. Tashjian, and J. H. Tashjian. New York: Plenum. Pp. 171–195.

Eränkö, O.; Palkama, A. (1961): Improved localization of phosphorylase by the use of polyvinylpyrolidone and high substrate concentration. J. Histochem. Cytochem. **9**, 585.

Folk, G. E.; Semken, H. A., Jr. (1991): The evolution of sweat glands. Int. J. Biometeorol. **35**, 180–186.

Gisolfi, C. V.; Sato, K.; Wall, P. T. (1985): Monkey model and techniques for studying eccrine sweating in man. In: Models in dermatology. Ed. by H. I. Maibach and N. J. Low. New York, Basel: Karger. Pp. 117–125.

Gomori, G. (1952): Microscopic histochemistry. Chicago: University of Chicago Press.

Hyndman, O. R.; Wolkin, J. (1941): Sweat mechanism in man: study of distribution of sweat fibers from sympathetic ganglia, spinal roots, spinal cord and common carotid artery. Arch. Neurol. Psychiat. **45**, 446–467.

Johnson, G. S.; Elizondo, R. S. (1974): Eccrine sweat gland in *Macaca mulatta*: physiology, histochemistry, and distribution. J. Appl. Physiol. **37**, 814–820.

Kuno, Y. (1956): Human perspiration. Springfield, IL: Thomas.

Lillie, R. D. (1954): Histopathologic technic and practical histochemistry, 2nd ed. New York: McGraw-Hill.

Machida, H.; Giacometti, L. (1968): The skin. In: Biology of the howler monkey. Ed. by. M. R. Malinow. Basel: Karger. Pp. 126–140.

Machida, H.; Perkins, E.; Hu, F. (1967): The skin of primates. XXXV. The skin of the squirrel monkey (*Saimiri sciurea*). Am. J. Phys. Anthrop. **26**, 45–54.

Machida, H.; Perkins, E.; Montagna, W. (1964): The skin of primates. XXIII. A comparative study of the skin of the green monkeys (*Cercopithecus aethiops*) and the Sykes monkey (*Cercopithecus mitits*). Am. J. Phys. Anthrop. **22**, 453–465.

Martin, R. D. (1982): Et tu, tree shrew? Natural History **91** (8), 26–33.

Montagna, W.; Machida, H. (1966): The skin of primates. XXXII. The Philippine Tarsier (*Tarsius syrichta*). Am. J. Phys. Anthrop. **25**, 71–84.

Montagna, W.; Parakkal, P. (1974): The structure and function of skin. 3rd ed. New York: Academic Press.

Montagna, W.; Yun, J. S. (1964): The skin of primates. VIII. The skin of the Anubis baboon (*Papio doguera*). Am. J. Phys. Anthrop. **20**, 131–141.

Montagna, W.; Yun, J. S.; Machida, H. (1964): The skin of primates. XVIII. The skin of the rhesus monkey. Am. J. Phys. Anthrop. **22**, 307–320.

Montagna, W.; Yun, J. S.; Silver, A. F.; Quevedo, W. C., Jr. (1962): The skin of primates. XIII. The skin of the tree shrew (*Tupaia glis*). Am. J. Phys. Anthrop. **20**, 431–440.

Nakamura, Y.; Hatanaka, K. (1958): Effect of denervation of the cat's sweat glands on their responsiveness to adrenaline, nicotine, and mecholyl. Tohoku. J. Exper. Med. **68**, 225–237.

Pinsky, L.; DiGeorge, A. M. (1966): Congenital familial sensory neuropathy with anhydrosis. J. Pediat. **68**, 1–13.

Perkins, E. M., Jr. (1966): The skin of primates. XXXI. The skin of the black-collared tamarin (*Tamarinus nigricollis*). Am. J. Phys. Anthrop. **25**, 41–70.

— (1968): A histological and histochemical survey of the skin of New World monkeys. Ph. D. thesis, Univ. Oregon Medical School, Portland.

Perkins, E. M.; Machida, H. (1967): The skin of primates. XXIV. The skin of the golden spider monkey (*Ateles geoffroyi*). Am. J. Phys. Anthrop. **26**, 35–43.

Rafel, E.; Alberca, R.; Bautista, J.; Navarrete, M.; Lazo, J. (1930): Congenital insensitivity to pain with anhidrosis. Muscle and Nerve **3**, 216–220.

Reay, D. A.; Thiele, F. A. J. (1977): Heat pipe theory applied to a biological system: quantification of the role of the "resting" eccrine sweat gland in thermoregulation. J. Theor. Biol. **64**, 789–803.

Robertshaw, D.; Taylor, C. R.; Mazzia, L. M. (1973): Sweating in primates: secretion by the adrenal medulla during exercise. Am. J. Physiol. **224**, 678–681.

Sakurai, M.; Montagna, W. (1964): Pharmacological properties of the sweat glands of *Lemur mongoz*. J. Invest. Dermatol. **42**, 411–414.

— — (1964): Experiments in sweating on the palms of the green monkey (*Cercopithecus aethiops*). J. Invest. Dermatol. **43**, 279–285.

— — (1965): Observations on the sweat glands of *Lemur mongoz* after denervation. J. Invest. Dermatol. **44**, 87–92.

Sato, K.; Sato, F. (1981): Pharmacologic responsiveness of isolated single eccrine sweat glands. Am. J. Physiol. **240**, R44–51.

Silver, A.; Montagna, W.; Versaci, A. (1964): The effect of denervation on sweat glands and Meissner corpuscles of human hands. J. Invest. Dermatol. **42**, 307–324.

Silver, A.; Versaci, A.; Montagna, W. (1963): Studies of sweating and sensory function in cases of peripheral nerve injuries of the hand. J. Invest. Dermatol. **40**, 243–258.

Smith, A. A. (1969): The palmar sweat glands of the rhesus monkey. Ph. D. thesis, University of Oregon Medical School, Portland.

Smith, A. A.; Dobson, R. L. (1966): Sweating and glycogenolysis in the palmar eccrine sweat glands of the rhesus monkey. J. Invest. Dermatol. **47**, 313–316.

Smith, A. A.; Perkins, E. M.; Machida, H. (1966): Durable mounts of the iodine stain for the phosphorylase reaction. Stain. Technol. **41**, 346–348.

Swanson, A. G. (1963): Congenital insensitivity to pain with anhydrosis. Arch. Neurol. **8**, 299–306.

Taylor, N. A. (1986): Eccrine sweat glands. Adaptations to physical training and heat acclimation. Sports Med. **3**, 387–397.

Thiele, F. A. J.; Hemels, H. G. M.; Malten, K. E. (1972): Skin temperature and water loss by skin. Trans. St. John's Hospital Dermatol. Soc. **58**, 218–223.

Torii, M.; Yamasaki, M.; Sasaki, T.; Nakayama, H. (1991): Functional differentiation of thermoregulation. Ann. Physiol. Anthropol. **10**, 163–170.

Uno, H.; Montagna, W. (1975): Catecholamine-containing nerve terminals of the eccrine sweat glands of macaques. Cell. Tiss. Res. **58**, 1–13.

Valen, L. van (1965): Treeshrews, primates, and fossils. Evolution **19**, 137–151.

Wada, M. (1950): Sudorific action of adrenaline on the human sweat glands and determination of their excitability. Science **111**, 376–377.

Wolf, J. E.; Maibach, H. I. (1974): Palmar eccrine sweating – the role of adrenergic and cholinergic mediators. Brit. J. Dermatol. **91**, 439–446.

Author's address: Dr. Allen A. Smith, School of Podiatric Medicine, Barry University, Miami Shores, FL 33161, USA

Z. Säugetierkunde 58 (1993) 330–336

ISSN 0044-3468

Utilisation des gîtes par la fouine *(Martes foina)* dans le Jura suisse

Par NICOLE LACHAT FELLER

Institut de Zoologie, Université de Neuchâtel, Neuchâtel, Suisse

Reception du Ms. 27. 12. 1992
Acceptation du Ms. 5. 4. 1993

Abstract

Use of resting sites by Stone martens (Martes foina) in the Swiss Jura mountains

Studied nine stone martens *(Martes foina)* by radiotracking. The animals (8 adults, 1 juvenile) were tracked from December 1986 to November 1991, for periods ranging from seven days to six months. Fifty-nine resting sites were used on 518 occasions. More than 90 % of them were located in buildings. Nests were made of straw in more than 80 % of the locations examined. Selection of resting sites was statistically associated with sex of the animal and with season.

Introduction

Depuis plusieurs années, l'anthropophilie de la fouine suscite l'intérêt de nombreux chercheurs. Que ce soit à la campagne (WAECHTER 1975; SKIRNISSON 1986) ou en ville (TESTER 1987; MÜSKENS et al. 1989), ce caractère a été vérifié à maintes reprises. Mais la fouine peut également vivre en milieu typiquement forestier (HEPTNER et NAUMOV 1974; LABRID 1983; SKIRNISSON 1986). Il paraissait dès lors intéressant d'étudier le cas du Jura suisse où la fouine a la possibilité de vivre soit en commensale de l'homme (dans des bâtiments ruraux où elle trouverait facilement à la fois gîte, chaleur et nourriture), soit en milieu naturel, forestier ou semi-ouvert.

Dans ce but, la situation des gîtes, à savoir les milieux choisis ont été étudiés et les différents gîtes ont été caractérisés, de manière à déterminer dans quelle sorte de matériau la fouine établissait son nid. La fréquence d'utilisation des gîtes, l'usage simultané de plusieurs d'entre eux, le taux de retour à ces gîtes ainsi que d'éventuelles préférences (individuelles ou par sexe) ont été examinés.

De plus, le choix des gîtes en fonction des saisons, de la météo et l'existence d'abris temporaires ont été mis en évidence.

Matériel et méthodes

Cette étude est réalisée dans le Jura suisse (N-W du canton de Berne), à la frontière avec les cantons de Neuchâtel et du Jura (47° 09′ N, 6° 56′ E). Il s'agit d'une zone de 30 km² dont l'altitude varie entre 900 et 1290 mètres. Ce terrain de La Chaux d'Abel a déjà été décrit par MARCHESI et al. (1989). La fouine y trouve de nombreuses possibilités de gîtes, au coeur même de ses terrains de chasse.

9 fouines (5 ♀, 3 ♂ et 1 juvénile) ont été suivies par radio-télémétrie, sur une période allant de décembre 1986 à novembre 1991. La durée des suivis a varié de 7 jours à 6 mois selon les individus.

Chaque fouine était pointée quotidiennement, de manière à connaître l'endroit où elle se tenait durant la journée. De plus, elle était régulièrement suivie durant ses activités nocturnes (une fois par semaine, du crépuscule à l'aube), pour connaître entre autres les abris temporaires où elle passait un certain temps entre 2 périodes de chasse.

Le relevé de traces sur la neige a permis d'affiner la connaissance des gîtes utilisés (passages empruntés) et de vérifier si ceux-ci étaient utilisés par d'autres animaux (fouines, chats *Felis catus*).

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5806-0330 $ 02.50/0

Dans les habitations, la localisation plus précise des nids a été réalisée grâce à la recherche de «toilettes». En effet, une fouine dépose souvent des excrêments en tas aux environs de son nid.

En règle générale, les nids occupés n'ont pas été inspectés de tout près afin de ne pas déranger l'animal et d'éviter de le voir déménager. Les nids connus mais délaissés à certaines périodes ont par contre été examinés de plus près. Un grand nombre ont été réutilisés par la suite. Cinq milieux pouvant abriter un gîte ont été recensés: grange (liée à une habitation), remise ou hangar, maison d'habitation (et ses alentours immédiats), pâturage boisé, forêt.

Pour chacune de ces catégories, différentes possibilités de localisation du nid ont été établies: dans la paille, dans le foin, dans un plancher ou un toit, dans un tas de bois ou de branches, dans une cavité au sol, dans un mur de pierres sèches, dans un arbre, dans un endroit non identifié.

Résultats

La radio-télémétrie a permis d'établir 518 utilisations de 59 refuges diurnes localisés avec plus ou moins de précision (Tab. 1).

Tableau 1. **Fréquence des gîtes dans les différents types de milieux**

	A	B	C	D	E	N	%[1]	%[2]
1	297	78				375	72,4	81,2
2		27	9		1	37	7,1	8
3				23		23	4,5	5
4		16				16	3,1	3,5
5				8		8	1,5	1,7
6		1			1	2	0,4	0,4
7			1			1	0,2	0,2
8	35	21				56	10,8	
Total	348	127	10	31	2	518	100	100
%	67,2	24,5	1,9	6	0,4			

A = grange; B = remise, hangar; C = pâturage; D = forêt; E = maison; 1 = paille; 2 = tas de bois; 3 = cavité au sol; 4 = foin; 5 = mur de pierres; 6 = plancher, toit; 7 = arbre; 8 = inconnu.
[1] ensemble des gîtes observés. – [2] gîtes identifiés avec précision.

Nature des gîtes

Les gîtes se situent en majorité dans des granges (67,2 %, N = 518) et des remises (24,5 %). Au total, 92,1 % des refuges utilisés sont recensés dans des constructions humaines. Les abris naturels (7,9 %) se trouvent soit en forêt (6 %), soit dans des pâturages boisés (1,9 %).

Il est intéressant de noter, qu'en moyenne, 64 % (♂: 60 %, ♀: 67 %) des gîtes «humains» disponibles sont utilisés, avec des variations de 43 à 100 % selon les individus. La disponibilité des gîtes «sauvages» est impossible à déterminer.

Sur l'ensemble de ces refuges, 44 ont été localisés avec certitude et identifiés (74,6 %, N = 59). Les 15 autres n'ont pu être déterminés assez précisément.

Les nids peuvent être constitués de matériaux fort divers mais l'on constate une préférence très significative pour la paille (81,2 %, N = 462; test binomial, $p < 0,00001$). Les tas de bois (8 %), les cavités au sol (5 %) de même que le foin (3,5 %) constituent eux aussi des abris recherchés.

Les murs de pierres sèches servent occasionnellement de gîtes (1,7 %) alors que les arbres ne sont utilisés qu'exceptionnellement (0,2 %), ainsi d'ailleurs que les planchers ou les toits des bâtiments (0,4 %).

Prises individuellement, toutes les fouines (N = 9), hormis une, montrent aussi une préférence pour la paille. Seule une femelle se distingue, privilégiant les tas de bois (58,3 %)

Tableau 2. **Fréquence d'occupation (en %) des gîtes pour chaque sexe (N = 462)**

	Mâles	Femelles
1	94,7	72
2	2,1	12
3	2,1	6,9
4		5,8
5		2,9
6	1,1	
7		0,4

1 = paille; 2 = tas de bois; 3 = cavité au sol; 4 = foin; 5 = mur de pierres; 6 = plancher, toit; 7 = arbre.

et les cavités au sol (38,9 %) (test exact de Fischer, $p < 0,0001$).

La localisation du nid diffère par contre passablement selon le sexe (Tab. 2). Les mâles utilisent plus souvent la paille et ils sont les seuls à avoir utilisé les planchers ou les toits. Inversement, le foin, les murs de pierres et un arbre n'ont été utilisés que par des femelles. Les tas de bois sont plus utilisés par les femelles, de même que les cavités au sol.

Occupation des gîtes

La fouine occupe plusieurs gîtes, répartis sur tout son territoire. Elle passe de l'un à l'autre, leur restant généralement fidèle durant de longues périodes (parfois plusieurs mois). Selon les individus, le gîte change presque tous les jours alors que d'autres peuvent utiliser le même plusieurs jours d'affilée (Tab. 3). Certains gîtes peuvent aussi être dédaignés sur de très longues périodes. C'est ainsi qu'une fouine utilisa un gîte 3 jours de suite puis n'y revint plus pendant 125 jours!

Un gîte peut aussi n'être occupé qu'une seule fois (17 cas recensés durant cette étude).

Le taux global de retour aux gîtes (rapport du nombre de retours dans un gîte déjà utilisé au moins une fois sur le nombre total d'utilisations de gîtes) est au total de 88,6 % (N = 518). Il est de 87,2 % pour les mâles (N = 235) et de 89,8 % pour les femelles (N = 283). Pour chaque sexe, les taux saisonniers de retour aux gîtes varient (Fig. 1).

Le genre de gîtes utilisés («humains» ou «sauvages») est très variable selon les individus (Tab. 4). Quatre fouines (N = 9) ne fréquentent que des gîtes «humains». Les cinq autres ont une majorité de gîtes «humains» mais aussi quelques gîtes «sauvages». Une seule femelle (FA26) montra une préférence pour les gîtes «sauvages» (56 % des utilisations, N = 39).

Il faut noter que les mâles habitent significativement plus de gîtes «humains» que les femelles (test exact de Fischer, p = 0,01). D'autre part, ils occupent en moyenne un plus grand nombre de gîtes (toutes catégories confondues) que les femelles (7,5/5,8) et le taux moyen d'utilisation d'un même gîte par un mâle est de 8,1 alors que chez une femelle il est de 10,5.

Tableau 3. **Exemples d'utilisation des gîtes**

Jour	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
Utilisation de 10 gîtes par FA 9																															
VII. 88										1	1	1	2	2	2	2		2		0			2		2	2	2		2		5
VIII. 88	2	2	3		2			3	3	2	3	3	2	0	2			2	4	5	2	2	2	2	2	4	2		6	2	
IX. 88	5	3	2	3	3	2	2	7	2	2		6		2	2					8	2	7	7	7		7	2		2	7	
X. 88			7	7	2		2				x	x	7	7	2		7	2	2	2	2	2		2	2	2	2	2	8		
XI. 88	8	0	8	8	7		2	2	7	8	9	7		8	1	8	1	1	1	1	1	10	10	10			10				
Utilisation de 4 gîtes par FA 17																															
XI.89																					1	1	1	1	2	1	1	1	1	1	
XII.89	1	1		3	1	1	1	1	1		1		1	1	1				1	1	x	x	1	1	1	1	1				1
I.90			1	1		1	1	1	1		1	1	1	1		1		1				1	4		1		1	1	1	1	
II.90	1																														

0 = animal à l'extérieur (contrôle durant la nuit); x = pas de signal.

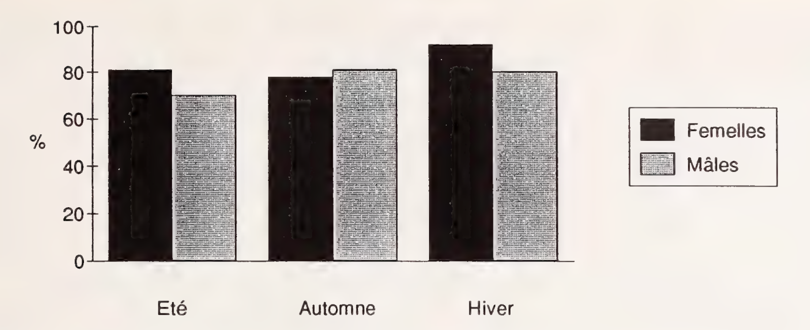


Fig. 1. Variations saisonnières du taux de retour à des gîtes déjà fréquentés. F = femelles, M = mâles

Finalement, certains gîtes ont été fréquentés par plusieurs fouines (dans le temps). C'est ainsi que si 59 gîtes ont été recensés tout au long de cette étude, seuls 47 d'entre eux n'ont été habités que par une des fouines étudiées.

Un certain nombre de gîtes peuvent servir de manière temporaire, entre les périodes de chasse nocturne. Ce sont des cachettes où la fouine se repose ou se met à l'abri. Il s'agit soit de gîtes utilisés également comme abris principaux, soit de gîtes différents ne servant que la nuit (exemples: racines d'arbres, lisière, buisson, mur de pierres sèches).

Tableau 4. **Nombre de gîtes utilisés par les différents individus**

	Gîtes »humains«	Gîtes »sauvages«	N
FA 7 (m)	12	0	12
FA 16 (m) juv.	3	0	3
FA 21 (m)	8	1	9
FA 25 (m)	5	1	6
Total (m)	28	2	30
FA 9 (f)	6	4	10
FA 17 (f)	4	0	4
FA 23 (f)	3	1	4
FA 24 (f)	3	0	3
FA 26 (f)	3	5	8
Total (f)	19	10	29
Total (m + f)	47	12	59

FA 7, FA 16, ... = identité des fouines; (m) = mâle; (f) = femelle.

L'utilisation des gîtes varie avec les saisons (Tab. 5). Si en hiver, les gîtes «humains» (tas de paille avant tout) sont nettement préférés (98,9 % des utilisations, N = 91), avec la belle saison, les gîtes naturels reprennent de l'importance, avec un maximum durant l'automne (19,4 %, N = 160). Toutefois, les gîtes «humains» restent les plus recherchés durant toute l'année (86,5 % en moyenne, N = 462).

On assiste également à une fluctuation du nombre de cachettes fréquentées durant l'année. Les fouines en utilisent un plus grand nombre en été et en automne.

Tableau 5. **Fréquence d'utilisation (en %) des gîtes en fonction des saisons (N = 462)**

	Hiver	Printemps	Eté	Automne	
1	95,6	84,2	77,6	76,9	x
2	1,1	15,8	6,2	13,1	
3			8,9	3,75	
4	1,1		4,7	3,75	x
5	2,2		2,6	1,9	
6					x
7				0,6	

1 = paille; 2 = tas de bois; 3 = cavité au sol; 4 = foin; 5 = mur de pierres; 6 = plancher, toit; 7 = arbre; x = gîtes »humains«.

Discussion

En Europe centrale et nord-occidentale, la fouine est connue de longue date comme étant une espèce anthropophile (Jensen et Jensen 1970; Waechter 1975; Rasmussen et al. 1986; Stubbe 1989). Dans le Jura suisse, la très grande majorité des refuges utilisés sont également situés dans des constructions humaines.

Selon la littérature, les endroits où les fouines se reposent peuvent être fort divers (Schmidt 1943; Waechter 1975; Krott 1985; Skirnisson 1986; Föhrenbach 1987; Herrmann 1987). Les fouines du Jura se sont bornées à utiliser des granges, des remises et des hangars. Seuls 2 cas d'utilisation d'autres structures de bâtiments (plancher, toit) ont été relevés. Cette constance peut s'expliquer de la manière suivante: dans une grange ou une remise, le nid se trouve le plus souvent sous des bottes de paille, à plusieurs mètres de profondeur, au sec, à l'abri des variations de température et préservé de tout dérangement.

Les tas de foin sont peu utilisés, probablement en raison de leur moins grande stabilité (foin entassé le plus souvent en vrac) et de l'utilisation plus rapide qu'en fait le paysan.

Le choix des gîtes «sauvages» est également assez restreint et ne concorde pas avec la grande variété évoquée par d'autres auteurs (Schmidt 1943; Waechter 1975; Labrid 1983; Skirnisson 1986; Föhrenbach 1987). Sur le terrain de La Chaux d'Abel, il s'agit la plupart du temps de tas de branches, d'espaces sous de vieilles souches ou de cavités ménagées parmi de grosses pierres.

La fréquentation des gîtes ne suit pas un modèle précis. Suite à ses déplacements nocturnes une fouine peut passablement s'éloigner de son gîte de départ. Il lui arrive dès lors souvent de ne pas dormir deux jours de suite à la même place. Elle évite de longs trajets de retour en dormant dans un gîte proche de l'endroit où sa chasse nocturne l'a menée. Ce phénomène a d'ailleurs aussi été vérifié pour la martre (Marchesi 1989).

Contrairement à d'autres auteurs (Labrid 1983; Skirnisson 1986), le taux de retour aux gîtes est très élevé sur l'ensemble de l'année, aussi bien pour les mâles que pour les femelles. Chez ces dernières, le taux hivernal (décembre à février) est très haut. Ceci peut être mis en relation avec la gestation de même qu'avec la météo (froid extrême, neige profonde).

Nous n'avons malheureusement pas de données concernant le printemps mais le taux estival (période d'élevage des jeunes) est toujours élevé. On assiste par contre à un léger fléchissement en automne, période où les jeunes s'émancipent.

Chez les mâles, le taux estival est le plus bas. C'est l'époque du rut et les mâles parcourent plus de distance, à la recherche de femelles, d'où une plus grande dispersion des gîtes et un taux de retour inférieur. En hiver, le taux augmente également. A cette saison les fouines mâles ne sélectionnent plus que des gîtes thermiquement intéressants. De même que chez les femelles, ce choix est certainement aussi influencé par des raisons météorologiques.

Les comportements varient beaucoup d'un individu à l'autre comme chez Skirnisson (1986). De réelles préférences individuelles n'ont toutefois pas pu être mises en évidence, hormis dans le cas d'une femelle.

Le nombre d'abris utilisés est très probablement lié à l'offre en gîtes et à la grandeur du domaine vital. Les mâles qui utilisent de plus grands territoires ont un plus grand nombre moyen de gîtes et par conséquent un taux moyen d'utilisation pour chacun plus faible que les femelles. Il existe toutefois une certaine concordance dans le nombre de gîtes entre les individus exploitant plus ou moins la même zone, simultanément ou à des époques différentes.

Les différences d'utilisation de chaque type de gîte en fonction du sexe sont difficiles à expliquer. Les femelles semblent rechercher des gîtes plutôt confortables, utilisables à long terme, alors que les mâles qui changent plus souvent d'endroits se contentent de gîtes moins attractifs.

Les fouines montrent un comportement ayant une grande valeur adaptative, en choisissant leurs abris en fonction des saisons. En hiver, les gîtes «humains» sont encore plus nettement préférés. Ceci confirme que la fouine montre un déterminisme d'ordre thermique dans la sélection de ses gîtes (Waechter 1975).

A la belle saison on assiste à un accroissement du nombre de gîtes «sauvages». Toutefois, il est intéressant de souligner que les gîtes «humains» gardent globalement le 1er rang tout au long de l'année. Durant l'été, lorsque les déplacements et les temps de chasse s'accroissent, les fouines multiplient leurs possibilités de refuges. Ces résultats coïncident avec ceux de Skirnisson (1986).

Remerciements

Ce travail fait partie d'une thèse de doctorat effectuée sous la direction du Prof. C. Mermod que je tiens à remercier ici. Ma reconnaissance va d'autre part à toutes les personnes qui, d'une manière ou d'une autre, ont permis la réalisation de ce travail et plus particulièrement au Dr J. M. Weber pour ses commentaires sur le manuscrit, à mes collègues et à tout le personnel de l'Institut de Zoologie, à Mme J. Moret, conseillère en statistiques ainsi qu'aux paysans de la Chaux d'Abel/Mont-Soleil et au garde-faune A. Hennet. Je suis également reconnaissante envers l'Inspectorat de la Chasse du Canton de Berne pour ses autorisations de piègeage.

Résumé

9 fouines (5 ♀, 3 ♂ et 1 juvénile) ont été suivies par radio-télémétrie, sur une période allant de décembre 1986 à novembre 1991. La durée des suivis a varié de 7 jours à 6 mois selon les individus.

518 utilisations de 59 gîtes ont été établies. 92,1 % des refuges fréquentés se trouvent dans des constructions humaines. Les fouines choisissent de préférence la paille pour y établir leur nid (81,2 %, N = 462). Des gîtes «sauvages» sont également utilisés, principalement durant la belle saison. La fréquentation des différents gîtes a été étudiée, de même que le taux de retour à ces gîtes qui est très élevé (88,6 % au total). Des variations ont été mises en évidence, selon le sexe des animaux considérés et selon les saisons. L'utilisation de gîtes temporaires ainsi que l'occupation (différée dans le temps) d'un même gîte ont été établies.

Zusammenfassung

Nutzung von Tagesverstecken bei Steinmardern (Martes foina) im Schweizer Jura

9 Steinmarder (5 adulte Weibchen, 3 adulte Männchen und 1 männliches Jungtier) wurden mit Hilfe der Radiotelemetrie von Dezember 1986 bis November 1991 untersucht. Die Beobachtungsdauer der einzelnen Tiere betrug 7 Tage bis 6 Monate. 518 Nutzungen von Tagesverstecken wurden registriert. 92,1 % aller Tagesverstecke lagen im menschlichen Siedlungsbereich. Als Nistmaterial bevorzugten die Steinmarder Stroh (81,2 %, N = 462). Tagesverstecke außerhalb des menschlichen Siedlungsbereiches wurden ebenfalls aufgesucht und insbesondere während der Sommerperiode genutzt. Die Besuchsfrequenz von 7 Verstecktypen wurde registriert. Hierbei wurden geschlechtsspezifische und saisonale Unterschiede deutlich. Die Stetigkeit, mit der einzelne Tagesverstecke aufgesucht wurden, war mit 88,6 % sehr hoch. Einige der Verstecke wurden nur temporär und von verschiedenen Tieren frequentiert.

Références

FÖHRENBACH, H. (1987): Untersuchungen zur Ökologie des Steinmarders (*Martes foina* Erxleben, 1777) im Alpen- und Nationalpark Berchtesgaden. Inaug.-Diss., Universität Heidelberg.

HEPTNER, V. G.; NAUMOV, N. P. (1974): Die Säugetiere der Sowjetunion. Band II. Jena:VEB G. Fischer Verlag.

HERRMANN, M. (1987): Zum Raum-Zeit-System von Steinmarderrüden (*Martes foina* Erxleben, 1777) in unterschiedlichen Lebensräumen des südöstlichen Saarlandes. Dipl.-Arbeit, Univ. Bielefeld.

JENSEN, A.; JENSEN, B. (1970): Husmarden *(Martes foina)* og marjagten i Danmark 1967/68. Danske Viltunders. **15,** 1–44.

KROTT, P. (1985): Weitere Bemerkungen über das Steinmardervorkommen (*Martes foina* Erxleben, 1777) im Kleinsölktal. Mitt. Abt. Zool. Landesmus. Joanneum **33,** 7–12.

LABRID, M. (1983): Etude de l'utilisation de l'espace et du temps par la martre *(Martes martes)* et la fouine *(Martes foina)* en forêt de Chizé (Deux-Sèvres) par la méthode du radio-tracking. D.E.A., Univ. Paris XIII.

MARCHESI, P. (1989): Ecologie et comportement de la martre (*Martes martes* L.) dans le Jura suisse. Thèse de doctorat, Univ. Neuchâtel.

MARCHESI, P.; LACHAT, N.; LIENHARD, R.; DEBIEVE, P.; MERMOD, C. (1989): Comparaison des régimes alimentaires de la fouine (*Martes foina* Erxl.) et de la martre (*Martes martes* L.) dans une région du Jura suisse. Revue suisse Zool. **96,** 281–296.

MÜSKENS, G. J. D. M.; MEUWISSEN, L. T. J.; BROEKHUIZEN, S. (1989): Simultaneus use of day-hides in beech martens (*Martes foina* Erxleben, 1777). In: Populationsökologie marderartiger Säugetiere. Ed. by M. STUBBE. Wiss. Beiträge Universität Halle, Pp. 409–421.

RASMUSSEN, A. M.; MADSEN, A. B.; ASFERG, T.; JENSEN, B.; ROSENGAARD, M. (1986): Undersøgelser over husmaren *(Martes foina)* i Danmark. Danske Viltundersogelser **41,** 1–39.

SCHMIDT, F. (1943): Naturgeschichte des Baum- und des Steinmarders. Leipzig: Verlag P. Schöps.

SKIRNISSON, K. (1986): Untersuchungen zum Raum-Zeit-System freilebender Steinmarder (*Martes foina* Erxleben, 1777). Beitr. Wildbiologie **6,** 1–200.

STUBBE, M. (1989): Baum- und Steinmarder *Martes martes* (L.) *Martes foina* (Erxleben). In: Buch der Hege. 1. Haarwild. Ed. by H. STUBBE. Frankfurt: Verlag Harri Deutsch. Pp. 478–502.

TESTER, U. (1987): Verbreitung des Steinmarders (*Martes foina* Erxleben) in Basel und Umgebung. Verhandl. Naturf. Ges. Basel **97,** 17–30.

WAECHTER, A. (1975): Ecologie de la fouine en Alsace. Rev. Ecol. (Terre Vie) **29,** 399–457.

Adresse de l'auteur: NICOLE LACHAT FELLER, Institut de Zoologie, Université de Neuchâtel, Chantemerle 22, CH-2007 Neuchâtel, Suisse

Z. Säugetierkunde 58 (1993) 337–343

ISSN 0044-3468

On the behavior of vicunas (*Vicugna vicugna* Molina, 1782)

Differences due to sex, season and proximity to neighbors

By G. E. Svendsen and P. C. Bosch

Department of Biological Sciences, Ohio University, Athens, Ohio, USA

Receipt of Ms. 31. 7. 1991
Acceptance of Ms. 11. 5. 1993

Abstract

Investigated the behavior of adult, territorial males and the associated females in a high-density population at the Pampa Galeras National Vicuna Reserve and a low-density population near Arequipa in the southern Peruvian puna comparing the breeding season (February–April) with the non-breeding season (August–September). Data were collected by the focal sample procedure using a 1-h observation period. Thirteen categories of behavior were used, "graze", "lookup", "alert", "roll", "lie", "groom", "walk", "run", "chase", "defecate-urinate", "threat", "standoff", and "nurse". A time budget was used to compare behaviors under different conditions. The behavior of male vicunas during the breeding seasons was both quantitatively and qualitatively different than behavior displayed during the non-breeding season. Males performed all behaviors at a higher rate during the breeding season. The behaviors of females differed quantitatively between seasons. Hypotheses dealing with female cooperation and defense of resources were rejected. The proximity of neighbors affected the behavior of both males and females. Females spent more time in alert when neighbors were present, males grazed less and spent more time performing behavior associated with repelling intruders.

Introduction

Vicunas are ungulates (Family Camelidae) that inhabit the high-altitude andean puna. Their social organization is characterized by three types of social groupings: families that tend to remain resident in one area throughout the year, groups of bachelors that wander over a large area, and solitary males. Each family consists of a single adult resident male, one to several females, and young of the year. Resident males act agonistically towards other males and defend a territory year-around (Koford 1957; Franklin 1974, 1978, 1983; Bosch and Svendsen 1987). Breeding occurs over a well-defined period from late February through April (Hofman et al. 1983). The mating system is polygynous with about three females associated with each resident male. All indications are that females only mate with the resident male with which they are associated (Koford 1957; Franklin 1974, 1978, 1983; Menard 1982; Hofman et al. 1983; Bosch and Svendsen 1987).

The objectives of this research were to describe the behavior of adult, resident male and female vicunas and to characterize similarities and differences between them, to quantify how behavior was influenced by season of the year (breeding season vs non-breeding season) and by density (high density vs low density), and to test two hypotheses dealing with the role of the female in the group (intragroup cooperation and defense of resources).

Material and methods

Populations

The study was carried out in the southern Peruvian puna. The density of the Pampa Galeras population (PG) at the Pampa Galeras National Vicuna Reserve, Department of Ayacucho, was about 0.5 per ha based on the 1980–81 census. The density of this population was sufficiently high so that

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5806-0337 $ 02.50/0

available pasture was occupied completely by resident territorial males and their associated females and young. Territories abutted one another and neighbors were always in view. Bachelor groups wandered over the area daily. The Coppermine population (CM) was located northeast of Arequipa, Department of Arequipa. The density was unknown, however it was sufficiently low so that available pasture was not occupied completely. Some families were isolated, and the borders to the territories of these resident males did not abut. Seven families in the CM population whose territory did not abut with the territory of others and whose nearest neighbors were usually out of sight were selected and are used in the analysis.

Seasons

Data were collected during two periods designated as the breeding season (March–April–May) and the nonbreeding season (August–September) in 1982 and 1983 (Hofman et al. 1983).

Observations

Observations were made in the relatively flat, treeless terrain with binoculars and data were recorded either in written field notes or with the aid of a tape recorder. Field work was restricted between sunrise and noon during March and April because of afternoon storms. After mid-April when afternoon storms ceased, observations were made throughout the day. Vicunas were classified as resident male (males holding a territory), bachelor male (nonresident males in bachelor groups), adult females, and young (Bosch and Svendsen 1987). Only data collected on adult males and adult females were used in this analysis.

Behaviors

Thirteen categories of behavior were used. "Graze" included all feeding behavior. "Lookup" included all looking around except for the more intense "alert" in which vicunas looked with head raised and ears erect. "Roll" in the dirt was separated from "lie". "Groom" included scratching the body with either the forefoot or hindfoot as well as biting and chewing the fur. Locomotory categories included "walk", "run", and "chase". "Defecate-urinate (DU)" represented all elimination at dung piles or elsewhere. "Threat" was characterized by an erect body posture with ears laid back and head held high. The display by males interacting with one another at their territory boundaries was termed "standoff". Suckling by young was called "nurse". When a male directed movements of females in his territory, it was termed "herding".

Sampling

Time budgets were determined for individual resident vicunas using the focal sample procedure. All observations were made on residents while they were within the boundary of their home territory. A focal sample consisted of a 1-h observation period on a single vicuna, the duration of each behavior was recorded in seconds. Only data on resident males and females were included in this analysis. During the breeding season at Pampa Galeras, data were gathered on 23 vicuna families in a random manner. Different families were studied on different days throughout the week. During the following week, some families were resampled, some were not. Within a given day, vicunas from 2 to 5 different families were studied. A common procedure was to select a family and gather data on the male and 1 or 2 females, then move on to another family. There were sufficient vicuna families in the study area so that it was not necessary to gather data on the same family group repeatedly. Data for the nonbreeding season at Pampa galeras were gathered on 8 different vicuna families. Seven different families were studied at the Coppermine site. A single focal sample was collected on each male and 1 or 2 of the females in each family. Each 1-h focal sample is treated as an independent sample in the analysis. The only criteria used for selecting a family to study was that it included a male and at least one female. The size of the families studied ranged from 2 to 7 ($\bar{y}$ = 3.9 ± 1.97). Data used to test the hypotheses were number of minutes of activity in a category of behavior per hour. Tests of various hypotheses were made using the Kruskal-Wallis test.

Results and discussion

Males vs females

Significant differences were found between males and females during the breeding season for all categories of behavior except "lie" (Tab. 1). Females spent more time in "graze", males more time in other categories of behavior (Tab. 2). Males spent significantly more time in "lookup" and "alert" than did females during the non-breeding season (Tab. 1),

Table 1. **Time budget for behaviors of male and female vicunas during the breeding season (BR), and the nonbreeding season (NBR) at Pampa Galeras, Peru**

Behavior category	Male BR	Male NBR	Female BR	Female NBR
Graze	2668 ± 516	2934 ± 252	3273 ± 252	3323 ± 176
Lookup	276 ± 199*	107 ± 74	85 ± 85	59 ± 31
Alert	206 ± 233	255 ± 261	28 ± 62*	66 ± 109
Lie	65 ± 204	75 ± 212	67 ± 200	21 ± 6
Roll	7 ± 14	2 ± 6	4 ± 10*	1 ± 4
DU	31 ± 26	27 ± 24	9 ± 13	12 ± 10
Walk	198 ± 158	179 ± 131	81 ± 77	76 ± 54
Run	40 ± 66*	3 ± 9	6 ± 13	2 ± 4
Chase	23 ± 32	11 ± 16		
Threat	4 ± 11	0	5 ± 20	0
Standoff	24 ± 94*	0		
Groom	15 ± 11*	4 ± 4	10 ± 12	6 ± 7
Nurse			25 ± 51	34 ± 63
	(N = 109)	(N = 8)	(N = 119)	(N = 20)

* significantly different between breeding and non-breeding seasons within sexes, Kruskal-Wallis ANOVA. N = number of 1 h focal samples. Data are given as mean and standard deviation.

whereas females spent more time in "graze" (Tab. 2). Both sexes visited dung piles to defecate and urinate ("DU"), kneaded the dung pile with their forefeet, and smelled the kneaded dung. Males visited the dung piles about 3 times more frequently that did females during the breeding season and about 2 times more frequently during the nonbreeding season.

In polygyny, a male's reproductive success is limited by the number of females he mates with, whereas the reproductive success of females depends on her ability to rear offspring (Geist 1971; Trivers 1972; Clutton-Brock et al. 1979, 1980). The behavior of male and female vicunas reflects these different roles. Males engaged in behaviors associated with vigilance, territorial display, and chases, whereas females eat. Female vicunas grazed 91 % of the time they were observed and males grazed 75 % of the time (Bosch and Svendsen 1987).

Behavioral differences were also evident in everyday activities such as "walk" and "DU" (Tab. 2). Walk is the normal way in which vicunas move about during the day. During the breeding season, males spent significantly more time in "walk" than did females. Males walked to visit dung piles, to herd females, and to check out the territory boundary. Family members use communal dung piles at which they defecate and urinate. Males defecate and urinate at dung piles more frequently than do females (Koford 1957). Franklin (1979, 1983) suggested that dung piles served as scent posts for the family members and were involved in maintaining the territory. The frequent visitation of dung piles by males in both the breeding and non-breeding seasons is consistent with the pattern of ter-

Table 2. **Comparison of the behavior of male and female vicunas in the breeding season (BR) with the non-breeding season (NBR) at Pampa Galeras, Peru**

Values for each category are given in table 1

Behavior category	BR	NBR
Graze	M < F	M < F
Lookup	M > F	M > F
Alert	M > F	M > F
Lie	M = F	M = F
Roll	M > F	M = F
Walk	M > F	M = F
DU	M > F	M = F
Run	M > F	M = F
Groom	M > F	M = F

Significance level, $p < 0.05$, Kruskal-Wallis ANOVA.

ritoriality where cues related to maintaining the territory are present throughout the year. Dung piles may contain cues for individual recognition and reproductive condition of the female.

Males and females spent the same amount of time in "walk" during the non-breeding season, however the context in which "walk" occurred in each was different. Males spent less time interacting with neighbors and bachelors during the non-breeding season, but still visited dung piles and territory boundaries. Females spent their time walking and feeding. Total time spent in "walk" by females was greater in the non-breeding season. Perhaps this was related to the quantity and quality of forage available and reflected more time searching for food.

Male: Breeding season vs non-breeding season

Significant differences were found between seasons for categories of behaviors of males associated with increased vigilance, chasing, and displays at territory boundaries (Tabs. 1, 3). "Threat" and "standoff" were recorded only during the breeding season, all other behaviors were performed more frequently during the breeding season.

Table 3. **Comparison of the behavior of male vicunas in the breeding season (BR) with the non-breeding season (NBR) at Pampa Galeras, Peru**

Values for each category are given in table 1

Behavior	Comparison
Graze	BR = NBR
Lookup	BR > NBR
Alert	BR = NBR
Lie	BR = NBR
Roll	BR = NBR
DU	BR = NBR
Walk	BR = NBR
Run	BR > NBR
Chase	BR = NBR
Threat	BR > NBR
Standoff	BR > NBR
Groom	BR > NBR

Significance level $p < 0.05$, Kruskal-Wallis ANOVA.

Table 4. **Comparison of the behavior of female vicunas in the breeding season (BR) with the non-breeding season (NBR) at Pampa Galeras, Peru**

Values for each category are given in table 1

Behavior	Comparison
Graze	BR = NBR
Lookup	BR = NBR
Alert	BR < NBR
Lie	BR = NBR
Roll	BR > NBR
DU	BR = NBR
Walk	BR = NBR
Run	BR = NBR
Threat	BR > NBR
Groom	BR = NBR
Nurse	BR = NBR

Significance level $p < 0.05$, Kruskal-Wallis ANOVA.

Female: Breeding season vs non-breeding season

Females spent more time in "alert" during the non-breeding season, and more time in "threat" and "roll" during the breeding season (Tabs. 1, 4).

Male: Male interactions

Fighting among vicunas did not occur frequently enough to be recorded in the sampling periods. However, fights were observed at other times. No fights were observed among females or among resident males, all fights observed occurred between resident males and bachelor males. Injuries due to these fights cannot be determined, but headlong chases did result in spectacular falls by both the pursued and pursuer. Bachelor males were observed with broken legs, dislocated hips, and open wounds, some of these could have resulted from fights or falls during chases.

Herding and positioning by the male

Male vicunas often directed members of their family to move in a particular direction or to a location within the territory "herding". "Herding" occurred most often during the breeding season, but it also occurred during the non-breeding season and at the low density site. A herding male moved toward the females and young, using threat displays toward individuals. Females that strayed from the group were directed back. A hesitant female received a bite to the rump. Males herded females from the edge of the territory to the middle, especially when a neighboring male was nearby or following "standoff" at a boundary.

Males spent more time in vigilence during the breeding season than they did during the non-breeding season. This was reflected in the amount of time spent in "alert" and "lookup". As the group moved through their territories on their daily activities, proximity to different neighbors changed. During the breeding season, males tended to position themselves between their females and the closest neighboring male. The position of various males with respect to the position of their females and neighboring males was determined over a several day sampling period at Pampa Galeras. Out of 52 sightings taken during the breeding season, 39 males were situated between their females and the closest male and 13 were not ($\chi^2 = 13$, $P < 0.05$), whereas out of 21 sightings taken during the non-breeding season, the numbers were 13 and 9 respectively ($\chi^2 = 0.7$, ns).

Females: Group cohesion and defense of resources

Vicunas normally walk through their territory during daily activities. Females walk while feeding, walk to dung piles, and walk to different regions of the territory. Females sometimes remained together and moved in unison with the male to one side, and at other times they were spread out and each female moved independently from the others. When two females came too close to one another, one or both responded with "threat". Females did not engage in social behaviors such as allogroom. Even licking of the young by a mother was an extremely rare event.

When intruders trespassed on the territory, resident females did not rush to chase the intruders off as did the male. Females continued to graze unless the chase came close. If the intruder was a non-group female that was trying to join the group, the females investigated the newcomer, made threats towards her, but did not drive her off. Females did not engage in displays at the boundaries, nor did they show other behaviors that could be interpreted as defense of the territory.

A female should try to prevent other females from joining a group unless there are advantages due to cooperation (Altmann et al. 1977) or the females are related (Hamilton 1964). Of the commonly cited advantages of group-living, only predator vigilance cannot be ruled out for female vicunas. Females performed no behaviors during the day that indicate cooperation in gathering food, defending resources, or caring for young.

Female philopatry characterizes group formation in many polygynous species of mammals (Greenwood 1980). Female young settle with or near their mother and may form matrilines (Armitage 1981). Franklin (1978) reported that vicunas expelled female young after about 10 months of age. However, we observed female young still present in the family 24 months after birth, and young as old as 16 months were allowed to suckle. Menard (1982) reported similar findings. We suggest that philopatry may be involved in the formation of the multifemale group, whereby females are able to increase their inclusive fitness by sharing the resources of a proven territory with female kin.

Table 5. **Time budget for behaviors of male and female vicunas during the breeding season at the Coppermine site**

Data are from 7 selected families without neighbors

Behavioral category	Male	Female
Graze	3015 ± 334	3397 ± 131*
Lookup	92 ± 36	38 ± 131*
Alert	140 ± 73	62 ± 68*
Lie	93 ± 222	36 ± 84
Roll	6 ± 10	3 ± 4
DU	36 ± 28	16 ± 26
Walk	205 ± 119	37 ± 24*
Run	5 ± 8	3 ± 7
Chase	2 ± 4	
Threat		
Standoff		
Groom	7 ± 8	9 ± 10
	(N = 7)	(N = 13)

* significantly different between males and females, Kruskal-Wallis ANOVA, significance level $p < 0.05$. N = number of 1 h focal samples. Data are given as mean ± standard deviation.

Table 6. **The behavior of male and female vicunas in the breeding season, comparing vicunas living in families with adjacent neighbors with vicunas living in families without neighbors (CM)**

Values for each category are given in tables 1 and 5

Behavioral category	Male	Female
Graze	PG < CM	PG < CM
Lookup	PG > CM	PG > CM
Alert	PG = CM	PG < CM
Lie	PG = CM	PG = CM
Roll	PG = CM	PG = CM
DU	PG = CM	PG = CM
Walk	PG = CM	PG > CM
Run	PG > CM	PG = CM
Chase	PG > CM	
Threat	PG > CM	PG > CM
Standoff	PG > CM	
Groom	PG = CM	PG = CM

Significance level, $p < 0.05$, Kruskal-Wallis ANOVA.

Behavior and proximity to neighbors

The presence of neighbors had a significant effect on the time budget of males during the mating season (Tabs. 5, 6). At Pampa Galeras (PG), resident males defended boundaries to territories that abutted two or three other territories. In addition, there were several bachelor groups using the area that intruded on the resident's territories. Each resident male monitored the position of its neighbors during the day and watched for intruders. At the Coppermine site (CM), the territories of resident males did not abut other territories. The nearest neighbors were out of sight, and no bachelor groups were present during the study. Males without neighbors grazed more and spent less time performing behaviors that repelled intruders. There was no significant difference in the time budgets for females at high or low density sites except for "alert". Females spent more time in "alert" at the high density site.

The differences in behavior between males and females observed at the high-density Pampa Galeras site were also evident at the low-density Coppermine site (Tab. 6). Males spent more time than females walking about, visiting dung piles and boundaries, and in "look up" and "alert". Males recognized a boundary to the territory whether or not neighbors were present, and differences in behavior were quantitative not qualitative.

Acknowledgements

This research was initiated through the Commission for Educational Exchange between the United States and Peru with support from the Fulbright-Hays Faculty Abroad Program to G. E. Svendsen. The Peruvian Ministerio de Agricultura y Alimentation, the Proyecto Especial Utilizacion Racional de la Vicuna, and friends and workers at the Pampa Galeras Reserve provided valuable assistance. World Wildlife Fund helped facilitate the research. Much of what we learned about the altiplano, its people, and vicunas came from two young friends and companions, Jose Luis Segovia Juarez and Esteban Gutmann. Ohio University provided support for analysis of data and manuscript preparation.

Zusammenfassung

Über das Verhalten von Vikunjas (Vicugna vicugna Molina, 1782). Unterschiede bedingt durch Geschlecht, Jahreszeit und Entfernung zu Nachbarn

Das Verhalten von erwachsenen, männlichen Vikunjas unterschied sich quantitativ und qualitativ vom Verhalten der erwachsenen, weiblichen Vikunjas, und dieser Unterschied bestand während und außerhalb der Brunstzeit. Weibchen verbrachten mehr Zeit beim Grasen, während Männchen sich anderweitig beschäftigten. Das Verhalten der Männchen war auf Wachsamkeit gerichtet, das Vertreiben von Eindringlingen und die Markierung ihres Gebietes. Dieses Verhalten war jedoch häufiger während als außerhalb der Brunstzeit. Gebietstreue Männchen verteidigten ihr Gebiet das ganze Jahr über. Weibchen halfen dabei nie. Die Anwesenheit eines fremden Männchens erhöht die Verteidigungsbereitschaft der gebietstreuen Männchen. Dieses hatte jedoch keinen Einfluß auf das Verhalten der Weibchen.

References

Altmann, S. A.; Wagner, S.; Lennington, S. (1977): Two models for the evolution of polygyny. Behav. Ecol. Sociobiol. **2**, 397–410.

Armitage, K. B. (1981): Sociality as a life-history tactic of ground squirrels. Oecologia **48**, 36–49.

Bosch, P. C.; Svendsen, G. E. (1987): Behavior of male and female vicuna (*Vicuna vicuna* Molina, 1782) as it relates to reproductive effort. J. Mammalogy **68**, 425–429.

Clutton-Brock, T. H.; Albon, S. D.; Gibson, R. M.; Guinness, F. E. (1979): The logical stag: Adaptive aspects of fighting in red deer (*Cervus elaphus* L.) Anim. Behav. **27**, 211–225.

Clutton-Brock, T. H.; Albon, S. D.; Harvey, P. H. (1980): Antlers, body size and breeding group size in Cervidae. Nature **285**, 565–567.

Franklin, W. L. (1974): Social behavior of the vicuna. In: The behaviour of ungulates and its relation to management. Ed. by V. Geist and F. Walther. Morges, Switzerland: IUCN Publ., No. **24**, Pp. 447–487.

— (1978): Socioecology of the vicuna. Unpubl. Ph. D. diss., Utah State Univ., Logan, Utah.

— (1979): Territorial marking behavior by the South American vicuna. In: Chemical signals: vertebrates and aquatic insects. Ed. by D. Muller-Schwarze and R. M. Silverstein. New York: Plenum. Pp. 53–66.

— (1983): Contrasting socioecologies of South America's wild camelids: The vicuna and the quanaco. In: Advances in the study of mammalian behavior. Ed. by J. F. Eisenberg and D. G. Kleiman. Amer. Soc. Mammal., Spec. Publ. No. 7, 573–629.

Geist, V. (1971): Mountain sheep: A study in behavior and evolution. Chicago: University of Chicago Press.

Greenwood, P. J. (1980): Mating systems, philopatry, and dispersal in birds and mammals. Anim. Behav. **28**, 1140–1162.

Hamilton, W. D. (1964): The genetical evolution of social behaviour I, II. J. Theor. Biol. **7**, 1–59.

Hofman, R. K.; Otte, K.; Ponce, C. F.; Rios, M. A. (1983): El manajo de la vicuna silvestre. Zools. Deutsche Gesellschaft für Technische Zusammenarbeit, Dag-Hammerskjöld-Weg, D-6236 Eschborn/Ts. 1.

Koford, C. B. (1957): The vicuna and the puna. Ecol. Monogr. **7**, 153–219.

Menard, N. (1982): Quelques aspects de la socioecologie de la Vigogne *Lama vicugna*. Rev. Ecol (Terre Vie) **36**, 15–36.

Svendsen, G. E. (1974): Behavioral and environmental factors in the spatial distribution and population dynamics of a yellow-bellied marmot population. Ecology **55**, 760–771.

Trivers, R. L. (1972): Parental investment and sexual selection. In: Sexual selection and the descent of man. Ed. by B. Campell. Chicago: University of Chicago Press. Pp. 136–179.

West-Eberhard, M. J. (1983): Sexual selection, social competition, and speciation. Quart. Rev. Biol. **58**, 155–183.

Authors' address: Dr. Gerald E. Svendsen and Paul C. Bosch, Department of Biological Sciences, Ohio University, 107 Irvine Hall, Athens, Ohio 45701, USA

Z. Säugetierkunde 58 (1993) 344–351

ISSN 0044-3468

Changes in the range distribution of *Hippocamelus bisulcus* in Patagonia

By Norma Inés Díaz

Fundación Carl C:Zon Caldenius

Receipt of Ms. 22. 7. 1992
Acceptance of Ms. 23. 4. 1993

Abstract

The past geographical distribution of *Hippocamelus bisulcus* followed through early travel accounts, missionaries' reports and historical literature from 1592 to 1960, as well as archaeological information, provides evidence of the presence of this species in open vegetation zones such as the steppe. The data thus far available indicate that the ideas about the huemul being only restricted to forested habitats in the past must be revised.

Introduction

The huemul, *Hippocamelus bisulcus* (Molina, 1782) was formely found in the southern Andean region in Argentina and Chile, between 33° and 54° south latitude. In Chile, it is now found in the Nevados de Chillán area (approximately 37°S), and in the Provinces of Aysen and Magallanes (Povilitis 1978). In Argentina, it is recorded from Los Glaciares and Perito Moreno National Parks, Santa Cruz Province, and also from some areas of Los Alerces National Park in Chubut Province (I.U.C.N. 1982).

Given the huemul's vulnerability to human predation, it has been a relatively easy target for hunters with dogs. Livestock diseases, habitat degradation and competition with domestic animals are also important causes of the species' decline (Drouilly 1983; Povilitis 1979, 1982, 1983; Prichard 1902; Rau 1980; Texera 1974). The only population of huemul in the Chilean region of Nevados de Chillán that still occurs is critically endangered, and several small groups, first studied in the early 1970s, now appear extinct (Tony Povilitis, pers. com).

On the evidence of historical and archaeological data, the huemul seems to have also occupied open vegetation zones such as the steppe. Travelers, missionaries, explorers and ethnographers provide us with the first observations and descriptions of this mammal. Perhaps because of the large amount of material involved and the scattered nature of references, such a study has not been previously attempted.

Material and methods

The past geographical distribution of this species was studied through the use of early travel accounts, missionaries' reports and historical literature. A rigorous evaluation of these sources was required. The references were considered with utmost caution since the huemul was a new species to European travelers, and an uncritical use of the records would have easily led to unwarranted results. The observer's ability in identifying wildlife has been evaluated through a thorough analysis of the texts. References to "stag" or "deer" have been disregarded in zones where the *Ozotoceros bezoarticus* could have been mistaken for a *Hippocamelus bisulcus*.

Information has been catalogued from over 102 reports covering the period 1592–1960. Although early travelers provided the basic source material, many bibliographies from various sources also led to significant accounts.

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5806-0344 $ 02.50/0

Results and discussion

Bibliographical records are more abundant for the Andean region and the Magallanic channels due to the interest of European expeditions and the preference to settle in the latter region. Early travelers found only two natural ports in the Atlantic coast of Patagonia:

Deseado and San Julián. This resulted in a concentration of data in both areas, while vast regions of the territory remained unexplored for a long time. This led to the assumption that the huemul was a deer of the mountains and that it had always inhabited areas in proximity to rugged topography. However, SCLATER (1873) stated: "It may be objected that the name chilensis is inappropriate as the animal is more particularly Patagonian than Chilean."

As early as the voyages of CAVENDISH (LA HARPE 1801) and BYRON (HAWKESWORTH 1774) in 1591 and 1765 to the South Seas, deer were observed in Puerto Deseado (47°44′S, 65°54′W), and the same remark was made at the end of the last century by FRANCISCO P. MORENO (in: PRICHARD 1902; WOLFFSOHN 1910; OSGOOD 1943). Also a manuscript kept in the British Museum labeled "Add. M. 17603", possibly from the 18th century, describes the Atlantic coast of Patagonia and refers to the presence of deer in the same geographical area.

The question that remains is why the deer were not observed by most travelers in Puerto Deseado in historical times. This can be due to different factors: 1. It must be considered that these trips rarely had a naturalistic objective and that the final destination was the Strait of Magellan. 2. There is evidence of changes in the volume of the Deseado River producing substantial influence on the environment and consequently on the flora and fauna (BURMEISTER 1901). Studies on the Deseado formation attest to a deposit of temporary and intermittent stream typical of arid or semiarid regions (LOOMIS 1914).

During hydrographical works carried out in 1900, BURMEISTER (1901) found two small groups of huemuls (6 and 12 individuals each) in the plains of Santa Cruz Province (approx. 47° S, 69°–70° W). He described the zone as a series of grades and the predominant vegetation was represented by calafate (*Berberis* sp.), molle (*Schinus o'donelli*) and mata negra (*Verbena tridens*). A few years earlier, when explorers traveled to Río Negro Province, the species was observed near Victorica and Irigoyen mountains (approx. 47°S, 69°W), far from the forested region (ROA 1884). Coastal observations of importance were made in Bahía Camarones (44° S, 41° W), Chubut Province (VIEDMA 1972) and in the area between Santa Cruz River and the Strait of Magellan (VIEDMA 1837).

In the Chilean steppe of Magallanes Province, deer were found in Segunda Angostura (HERNÁNDEZ DE OVIEDO 1852), Laguna Blanca (BERTRAND 1886), in the eastern coast of the Strait of Magellan (GUERRERO VERGARA 1880), San Gregorio and in the zone between Punta Dungeness and Chabunco (PASTELLS 1920).

Archaeological information also reveals important evidence of a broader geographical distribution. Remains of cervids examined by ROSENDO PASCUAL (GONZÁLEZ 1960; MENGHIN and GONZÁLEZ 1954) from sites at Intihuasi, San Luis Province (32°10′S, 66°21′W) and Ongamira, Córdoba Province (30°51′S, 64°31′W) yielded bones of the genus *Hippocamelus*. Even though the species was not identified, it indicates a much broader distribution for any *Hippocamelus* species (*bisulcus* or *antisensis*) than previously known.

Further remains of cervids show the presence of this mammal at the site Cueva Grande del Arroyo Feo, Santa Cruz Province (46°56′S, 70°30′W) located quite far away from the woody Andean region (SILVEIRA 1979). Furthermore, works carried out at Piedra Museo, south of El Jaramillo, Santa Cruz Province (47°11′S, 67°08′W) yielded as yet unidentified cervid remains which still have no radiocarbon date (LAURA MIOTTI, pers. com.). The presence of huemul is also confirmed at archaeological sites located in ecotonal areas such

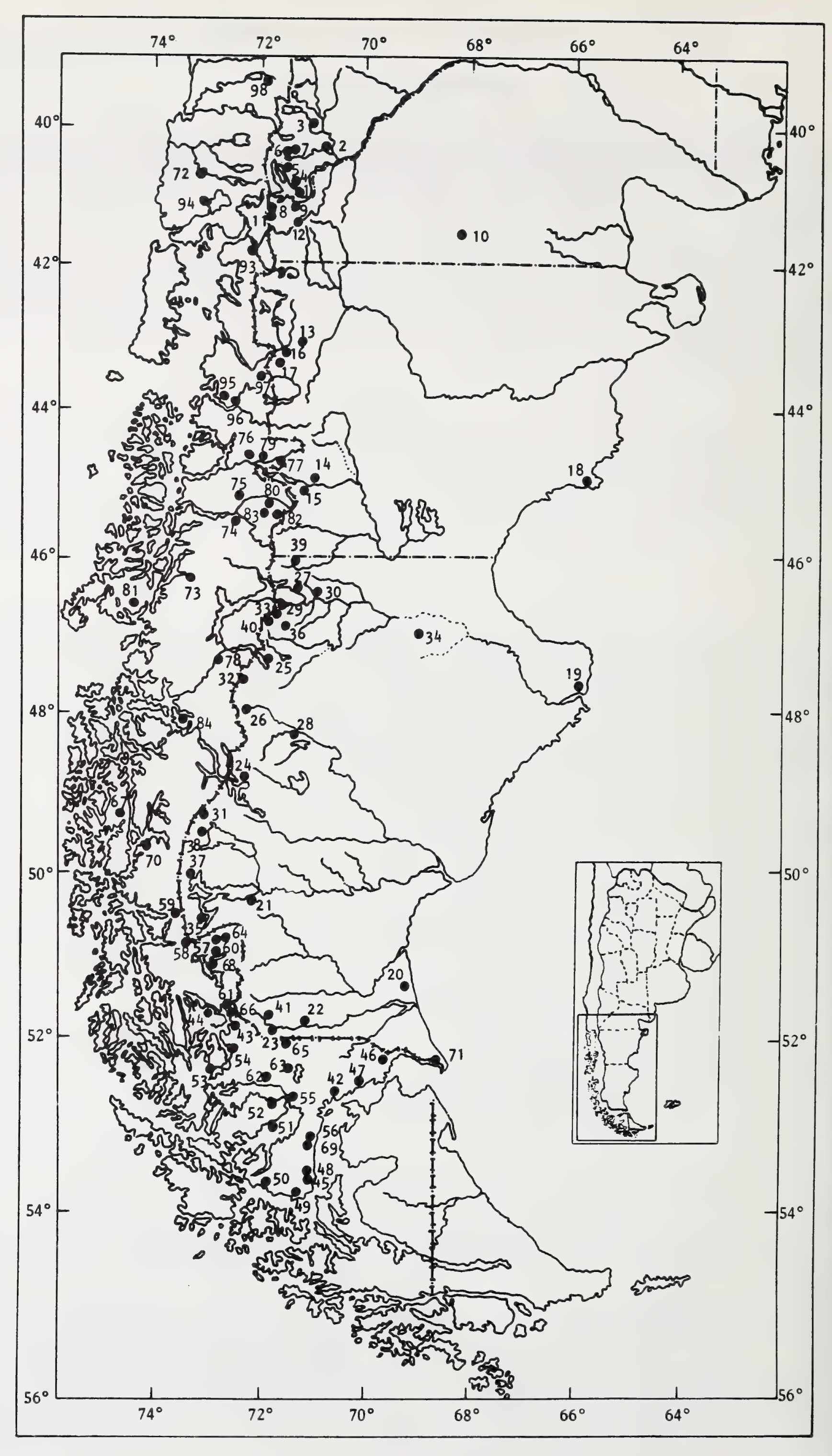


Fig. 1. Historical observations of huemul from 1592 to 1960. For location see opposite page

Argentina.

Neuquén: 1 = Puerto del Venado (41°01′S, 71°24′W), 2 = Confluence Caleufú River with Collón Curá (40°23′S, 70°45′W), 3 = Junín de los Andes (39°56′S, 71°05′W), 4 = Cuyín Manzano (40°47′S, 71°17′W), 5 = Northern Lake Traful (40°41′S, 71°13′W), 6 = Lake Falkner (40°28′S, 71°31′W), 7 = Lake Villarino (40°26′S, 71°35′W).

Río Negro: 8 = Boquete Pérez Rosales and Paso Barros Arana (41°05′S, 71°49′W), 9 = Sorroundings Nahuel Huapi (41°00′S, 71°30′W), 10 = Victorica and Irigoyen Mountains (41°41′S, 68°08′W), 11 = Western coast Lake Frías (41°04′S, 71°48′W), 12 = Nirihuau River (41°06′S, 71°08′W).

Chubut: 13 = Northern Thomas Peak (43°05′S, 71°10′W), 14 = Northern Guía Peak (45°05′S, 71°03′W), 15 = Senguerr River (45°02′S, 70°49′W), 16 = Futa-Leufú River (43°10′S, 71°45′W), 17 = 16 de Octubre (43°19′S, 71°18′W), 18 = Bahía Camarones (44°49′S, 65°41′W).

Santa Cruz: 19 = Puerto Deseado (47°44′S, 65°54′W), 20 = From Santa Cruz River to Strait of Magellan (approx. between 50°–52°S, 69°15′W), 21 = Lake Argentino (50°16′S, 72°28′W), 22 = Morro Philippi (51°44′S, 71°37′W), 23 = Gallegos River (51°52′S, 71°15′W), 24 = Northern coast Lake San Martín (49°11′S, 71°59′W), 25 = Lake Pueyredón (47°19′S, 72°00′W), 26 = Lake Belgrano (47°51′S, 72°06′W), 27 = Lake Buenos Aires (46°27′S, 71°28′W), 28 = Chico River (48°16′S, 71°22′W), 29 = Los Antiguos River (46°33′S, 71°37′W), 30 = Northern and eastern coast Lake Buenos Aires (46°33′S, 71°07′W), 31 = Fitz Roy (49°13′S, 73°05′W), 32 = Pirámide Peak (47°46′S, 72°26′W), 33 = Plateau between Los Antiguos and Jeinemeni Rivers (46°49′S, 71°40′W), 34 = Sorroundings Deseado River (approx. 47°S, 69°W), 35 = Glacier Moreno (50°31′S, 73°20′W), 36 = Southern Los Antiguos River (46°54′S, 71°32′W), 37 = Glacier Upsala (50°00′S, 73°24′W), 38 = Glacier Viedma (49°30′S, 73°20′W), 39 = Cholila (42°31′S, 71°27′W), 40 = Eastern coast Jeinemeni River (46°40′S, 71°40′W), 41 = SW of Santa Cruz province (51°21′S, 70°19′W).

Chile.

Magallanes: 42 = Segunda Angostura (52°35′S, 70°30′W), 43 = Punta de los Venados (52°20′S, 72°34′W), 44 = Bahía Worsley (51°40′S, 73°11′W), 45 = Punta Santa Ana (53°38′S, 71°00′W), 46 = Zone between Punta Dungeness and Chabunco (52°18′S, 68°32′W), 47 = San Gregorio (52°35′S, 70°09′W), 48 = Puerto Hambre (53°30′S, 71°00′W), 49 = Zone between Cerro Negro and Cabo Froward (53°54′S, 71°20′W), 50 = Puerto Gallant (53°40′S, 72°06′W), 51 = Englefield (53°05′S, 71°55′W), 52 = Riesco (53°00′S, 73°37′W), 53 = Sonda Obstrucción (52°14′S, 72°31′W), 54 = Bahía Pascua (52°28′S, 72°34′W), 55 = Hoyas Otway and Skyring (52°42′S, 71°33′W), 56 = Punta Arenas (53°08′S, 70°55′W), 57 = Payne (50°53′S, 73°00′W), 58 = SW Lake Argentino (50°40′S, 72°47′W), 59 = Glacier Francisco Vidal (50°42′S, 73°38′W), 60 = Cañadón de los Mosquitos (50°51′S, 72°35′W), 61 = Ultima Esperanza (51°32′S, 73°00′W), 62 = Carpa de Benavides (52°30′S, 72°00′W), 63 = Laguna Blanca (52°25′S, 71°09′W), 64 = Los Baguales (50°37′S, 72°28′W), 65 = Southern Gallegos River (52°08′S, 71°32′W), 66 = Tres Pasos (51°45′S, 72°21′W), 67 = Wellington (49°37′S, 74°40′W), 68 = Lake Sarmiento (51°04′S, 72°42′W), 69 = Río de los Ciervos (45°30′S, 71°00′W), 70 = Sorroundings Saumares Island (49°37′S, 74°00′W), 71 = Eastern coast Estrecho de Magallanes (52°0′S, 68°27′W).

Osorno: 72 = Osorno (40°33′S, 73°07′W).

Aysen: 73 = Huemules River (45°49′S, 73°34′W), 74 = Aysen River (45°24′S, 72°42′W), 75 = Southern Tabular Peak (45°08′S, 72°06′W), 76 = Cordón Huemules (44°40′S, 72°11′W), 77 = Southern Cáceres Peak (44°33′S, 71°26′W), 78 = Baker River (47°30′S, 73°37′W), 79 = Frías River (44°40′S, 72°00′W), 80 = Richards Peak (44°37′S, 71°30′W), 81 = Península Taitao (46°27′S, 74°00′W), 82 = Coyhaique (45°33′S, 72°03′W), 83 = Estero Mano Negra (45°24′S, 71°52′W), 84 = Glacier Jorge Montt (48°17′S, 73°30′W).

Santiago: 85* = Santiago (33°00′S, 34°12′W), 86* = San Bernardo (33°36′S, 70°44′W).

Colchagua: 87* = Cachapoal River (34°15′S, 69°55′W).

Maule: 88* = Bañados de Cauquenes (35°58′S, 72°21′W).

Concepción: 89* = Concepción (36°50′S, 73°03′W).

Bío, Bío: 90* = Bío Bío River (38°45′S, 71°27′W), 91* = Cuenca del Duqueco (38°46′S, 71°28′W), 92* = Antuco (37°20′S, 71°41′W).

Llanquihue: 93 = Southern Lake Taguatagua (41°42′S, 72°09′W), 94 = Sorroundings Frutillar (41°15′S, 73°01′W).

Chiloé: 95 = Palena River (43°58′S, 72°50′W), 96 = Confluence Palena and Frío Rivers (43°42′S, 72°19′W), 97 = Carrenleufú and Hielo Rivers (43°29′S, 71°46′W).

Valdivia: 98 = Pucón (39°16′S, 71°59′W).

Note: * Not indicated on the map due to a northern location.

as Alero Dirección Obligatoria (Rafael Goñi, pers. com.) and Cerro Casa de Piedra (Aschero 1981–82) Santa Cruz Province, Argentina.

The only site with archaeological evidence of huemul in the Chilean steppe is Alero Entrada Baker located at the origin of the Chacabuco River, Aysen, in layers corresponding probably to the beginning of the Christian era (Francisco Mena Larraín, pers. com.).

Nevertheless, it is the intention of the author not to suggest the existence of this species in the above areas based on assumptions but rather to await further fossil evidence and archaeological studies. As of the present state of knowledge, important points remain unanswered:

a. What kind of ecological events do the archaeological sites represent?
b. What dietary regimes were available?
c. How might environmental dynamics have influenced population densities and adaptations for reproduction?

Based on the records obtained, the figure shows 98 geographical sites from Argentina and Chile where the species was observed in the time span under study.

If the huemul once inhabited the Argentine plains (Carette 1922), reaching Uruguay in the Quaternay era (Kraglievich 1932), they could have reached Chile through accessible passes in a relatively recent time. When referring to the zone comprised between lakes Buenos Aires and Argentino, T. Hungerford Holdich (1904) stated that the presence of the huemul in the Chilean forest was an evidence that it had found its way through Andean passes.

Historical accounts for Argentina provide evidence that the population of huemul was extensive in four areas: Lake Tromen (Perea 1989), Lake Buenos Aires (Prichard 1910), Lake San Martín (S. Radboone in La Chacra 1936) and Lake Argentino (Prichard 1902; Kölliker et al. 1917). The number of animals observed in these zones contrasts greatly with the other areas, where generally only two or four individuals were found. On the other hand, it is surprising that the deer have only been recorded from Chile's coastal range in 1871 by the Corbeta Chacabuco in the surroundings of the Huemules River (approximately 46°S) (Simpson 1875).

In 1871 Enrique M. Simpson (1875) started an expedition 6.5 km south of Estuario Quitralco, Chile, with the intention of finding a pass across the cordillera, as the many deer observed in a valley made him suspect that they had come from Argentina where they were abundant. The importance of its presence in the zone was confirmed recently at archaeological sites in the river Ibañez valley (approx. 46°S), northern coast of Lake General Carrera–Buenos Aires (Francisco Mena Larraín, pers. com.).

Field information gathered in studies carried out recently in Aysen (44–49°S), Chile, show that the geographical distribution is in most cases intimately correlated to the eastern springs of the cordillera (Aldridge 1988).

Lydekker (1910) and Sclater (1873) considered the Argentine plains as the habitat of the huemul. If we take into account the zones where huemul abounded in the past, we find that in Santa Cruz two of the largest lakes (Buenos Aires and Argentino) are connected to important rivers that flow to the Atlantic Ocean, and that Lake San Martín lies close to the River Chico basin. Based on a review of the historical and archaeological information, it can be assumed that originally huemul inhabited the plains and that, considering their vulnerability, ecological changes, predators, human settlements or all of these together, the animals were compelled to migrate towards the mountains following the courses of the rivers or lakes. Something very similar could have happened in northern Patagonia where the higher human density could have prevented a more fluid dispersal of the species to Chile across the cordillera. In the surroundings of the Limay River, Neuquén Province, bone remains at excavations revealed the importance of this species as a faunal resource (Mario Silveira, pers. com.).

We may suppose that the huemul still occupy the niche to which they are best adapted. Modern studies are focussed on ecology, biology and conservation problems (ALDRIDGE 1988; DROUILLY 1983; POVILITIS 1979, 1983, 1985; RAU 1980; TEXERA 1974), but the survival of the species is still pending. The data presented in this study, on the other hand, are intended to show that all the ideas in the past about the huemul being only restricted to forested habitats will have to be revised.

This work supports the hypothesis that in the past the huemul lived in Patagonia gradually migrating eastwards to the Atlantic coast. The opposite alternative to the present hypothesis holds the misidentification of the species as probable. This argument is weakened because the southern border of distribution of *Ozotoceros bezoarticus* is in the north of Río Negro Province (CASAMIQUELA 1975) and a misidentification with *Pudu puda* is highly improbable.

Consequently, two alternatives must be considered:

1. Originally, the huemul lived in Patagonia and then retreated to the remote, undisturbed Andean areas. It is important to emphasize that the last registration of the huemul in the Atlantic coast date from the end of the 19th century when a strong anthropic influence took place. Analysis of a 10,000-year accumulation of owl pellets in Cueva Traful in southern Neuquén Province in Argentina enabled PEARSON (1987) to show that an important faunal change occurred during the last century. VEBLEN and LORENZ (1983) also reported prominent changes in vegetation during this period in the forest-steppe boundary in northern Patagonia.
2. The huemul lived in the Andean forested habitats and it occasionally reached the Atlantic coast. Environmental changes in the habitat may have initiated a migration of individual animals through corridors across inhospitable land (FORMAN and GODRON 1989). Pollen profiles covering the late and post-glacial era in Patagonia contain major vegetation changes that coincide with climatic fluctuations (MARKGRAF 1983).

Available information to date do not favour either of the alternatives, although neither of them can be dismissed until more controlled data and systematic studies are performed.

Zusammenfassung

Änderung des Verbreitungsgebietes von Hippocamelus bisulcus in Patagonien

Der Süd-Andenhirsch (*Hippocamelus bisulcus*) ist von 33°–54° südl. Br. in den patagonischen Anden Chiles und Argentiniens bis zur Magellanstraße beheimatet. Obwohl seine Verbreitungsgrenze nur ungenau bekannt war, vermutete man, daß sich diese Art nur auf das Andengebiet beschränkte.

Die frühere geographische Verbreitung dieser Hirschart wurde durch Berichte von Forschungsreisenden, Missionaren und Ethnographen belegt. Literatur wurde von 1592 bis 1960 in 102 Berichten berücksichtigt. Besonders hervorzuheben sind auch archäologische Knochenfunde dieses Hirsches in Patagonien.

Die vorliegende Arbeit erbringt den Nachweis dafür, daß der Süd-Andenhirsch früher auch die patagonische Steppe bewohnte.

References

I.U.C.N. (1982) South Andean Huemul. In: I.U.C.N. Mammal Red Data Book. Part 1. Ed. by J. THORNBACK and M. JENKINS. I.U.C.N. Publ., Gland. Pp. 477–481.

ALDRIDGE, D. K. (1988): Proyecto conservación del huemul (*Hippocamelus bisulcus*) en Chile. Medio Ambiente **9**, 109–116.

ASCHERO, C. A. (1981/1982): Nuevos datos sobre la arqueología del Cerro Casa de Piedra, sitio CCP5. Relaciones Soc. Arg. Antrop., Nueva Serie **14**, 267–284.

BERTRAND, A. (1886): Memoria sobre la rejión central de las tierras magallánicas. Anuario Hidrográfico de la Marina de Chile, Vol. **11**.

BURMEISTER, C. (1901): Memoria sobre el territorio de Santa Cruz. Ministerio Agricultura República Argentina.

CARETTE, E. (1922): Cérvidos actuales y fósiles de Sudamérica. Revisión de las formas extinguidas pampeanas. Rev. Mus. La Plata **26**, 393–475.

Casamiquela, R. M. (1975): Nota sobre la dispersión, en época histórica, de algunos mamíferos en el ámbito pampeano-patagónico. Relaciones Soc. Arg. Antrop., Nueva Serie **9**, 111–117.
Drouilly, P. (1983): Recopilación de antecedentes biológicos y ecológicos del huemul chileno y consideraciones sobre su manejo. Boletín Técnico 5. Santiago: Corporación Nacional Forestal.
Forman, R. T.; Godron, M. (1989): Landscape Ecology. New York: J. Wiley and Sons.
González, A. R. (1960): La estratigrafía de la gruta de Intihuasi (prov. San Luis) y su relación con otros sitios precerámicos de Sudamérica. Rev. Instituto Antropología 1, Apéndice II.
Guerrero Vergara, R. (1880): Los descubridores del Estrecho de Magallanes i sus primeros esploradores. Santiago de Chile.
Hawkesworth, J. (1774): Voyages autour du monde, entrepris par ordre de Sa Majesté Britanique, actuellement regnante, pour faire des découvertes dans l'Hemisphère austral. Exécuté successivement par le Chef d'escadre Byron, les capitaines Wallis, Carteret et Cook, dans les vaisseaux le Dauphin, l'Hirondelle et l'Endeavour. Rédigés par . . . sur les journaux tenus par les divers commandans et d'aprés les papiers de M. Joseph Banks. Traduit de l'anglois. Amsterdam.
Hernández de Oviedo y Valdes, G. (1852): Historia General y natural de las Indias, islas y tierra firme del mar Océano . . . Publícala la R. Academia de la Historia, cotejada con el códice original, enriquecida con las enmiendas y adiciones del autor e ilustrada en la vida y el juicio de las obras del mismo, por D. José Amador de los Ríos. Madrid.
Holdich, T. H. (1904): The countries of the King's Award. London: Hurst and Blackett.
Kölliker, A.; Kühn, F.; Reichter, F.; Tomsen, A.; Witte, L. (1917): Patagonia: resultados de las expediciones realizadas de 1910 a 1916. Buenos Aires: Sociedad Científica Alemana.
Kraglievich, L. (1932): Contribución al conocimiento de los cérvidos fósiles del Uruguay. An. Mus. Hist. Nat. **3**, 355–438.
La Harpe, J. F. de, comp. (1801): Abrégé de l'Histoire génerale des voyages de M. L'Abbé Prévot, contenant ce qu'il y a de plus remarquable, de plus utile et de mieux avéré dans les pays oú les voyageurs ont pénétré; les moeurs des habitants, la religion, les usages, arts et sciences, commerce, manufactures . . . Paris: Hotel de Thou. 1780-IX.
Loomis, F. B. (1914): The Deseado Formation of Patagonia. Eight Amherst Expedition. Mass.: Amherst College.
Lydekker, R. (1910): General sketch of the hoofed mammals. Harmsworth Natural History. London: Carmelite House.
Markgraf, V. (1983): Late and post-glacial vegetational and paleoclimatic changes in subantarctic, temperate, and arid environments in Argentina. Palynology **7**, 43–70.
Menghin, O.; González, A. R. (1954): Excavaciones arqueológicas en el yacimiemnto de Ongamira, Córdoba (Rep. Arg.), con apéndice por Rosendo Pascual. Not. Mus. La Plata, Antrop. **67**, 213–274.
Osgood, W. H. (1943): The mammals of Chile. Field Mus. Nat. Hist., Zool. Ser. **30**, 1–268.
Pastells, P. (1920): El descubrimiento del Estrecho de Magallanes. En conmemoración del IV Centenario, por . . . con la colaboración del Rvdo. P. Constantino Bayle. Madrid: Sucesores de Rivadeneyra.
Pearson, O. P. (1987): Mice and the post-glacial history of the Traful Valley of Argentina. J. Mammalogy **68**, 469–478.
Perea, E. (1989): . . . y Félix Manquel dijo . . . Textos Ameghinianos. Fundación Ameghino. República Argentina.
Povilitis, T. (1978): The Chilean Huemul Project – a case history (1975–76). In: Threatened Deer, Proceedings of a Working Meeting of the SSC Deer Specialist Group, Longview, Washington, U. S. A., 26 Sept.–1 Oct., 1977. I.U.C.N., Switzerland. Pp. 109–129.
— (1979): The Chilean huemul project (1975–1976): Huemul ecology and conservation. Ph. D. diss., Colorado State Univ., Fort Collins.
— (1982): The huemul in Chile: National symbol in jeopardy? Oryx **17**, 34–40.
— (1983): Social organization and mating strategy of the huemul (*Hippocamelus bisulcus*). J. Mammalogy **64**, 156–158.
— (1985): Social behavior of the Huemul (*Hippocamelus bisulcus*) during breeding season. Z. Tierpsychol. **68**, 261–286.
Prichard, H. H. (1902): Field notes upon some of the larger mammals of Patagonia, made between September 1900 and June 1901. Proc. Zool. Soc. Lond. Pp. 272–277.
— (1910): Hunting camps in woods and wilderness. London.
Rau, J. (1980): Movimiento, hábitat y velocidad del huemul del sur (*Hippocamelus bisulcus*) (Artiodactyla, Cervidae). Not. Mens. Mus. Nac. Hist. Nat. (Santiago) **24**, 7–9.
Roa, L. O. de (1884): Exploraciones de la Patagonia. Bol. Inst. Geog. Arg. **5**.
Sclater, P. L. (1873): Remarks on *Cervus chilensis* and *Cervus antisensis*. Ann. and Mag. Nat. Hist. **11**.
Silveira, M. J. (1979): Análisis e interpretación de los restos faunísticos de la Cueva Grande del Arroyo Feo (Pcia. de Santa Cruz). Relaciones Soc. Arg. Antrop. **13**, 229–247.

Simpson, E. M. (1875): Exploraciones hechas por la corbeta Chacabuco. Anuario Hidrográfico de la Marina de Chile. Vol. **1**.

Texera, W. D. (1974): Algunos aspectos de la biología del huemul (*Hippocamelus bisulcus*) (Mammalia: Artiodactyla, Cervidae) en cautividad. Anal. Inst. Patagonia, Punta Arenas (Chile) **5**, 155–188.

Veblen, T.; Lorenz, D. (1988): Recent vegetation changes along the forest/steppe ecotone of Northern Patagonia. Ann. Assoc. Am. Geog. **78**, 93–111.

Viedma, A. de (1837): Decripción de la costa meridional del sur, llamada vulgarmente patagónica . . ., Colección de Angelis, Vol. **6**.

— (1972): Diario de un viaje a la costa de Patagonia. Colección de Angelis, Edit. Plus Ultra. Vol. **8**.

Wolffsohn, J. W. (1910): Notas sobre el huemul. Rev. Chil. Hist. Nat. **14**, 227–234.

Author's address: Norma Inés Díaz, Tupac-Amarú 1011, RA-1407 Buenos Aires, Argentina

Z. Säugetierkunde 58 (1993) 352–361

ISSN 0044-3468

Allozyme diversity within and among populations of three ungulate species (*Cervus elaphus, Capreolus capreolus, Sus scrofa*) of Southeastern and Central Europe

By G. B. Hartl, G. Markov, Angelika Rubin, S. Findo, G. Lang, and R. Willing

Forschungsinstitut für Wildtierkunde und Ökologie der Veterinärmedizinischen Universität Wien, Österreich

Receipt of Ms. 26. 10. 1992
Acceptance of Ms. 8. 2. 1993

Abstract

75 red deer, 121 roe deer, and 155 wild boars from several sampling sites in Bulgaria were examined for genetic variability and differentiation at 40–43 isozyme loci by means of horizontal starch gel electrophoresis. For comparison with Central European populations 103 red deer, 106 roe deer and 70 wild boars from sampling sites in Slovenia, Austria, Slovakia, and France were screened additionally. Mean P (proportion of polymorphic loci, 99 per cent criterion) in the red and the roe deer was 18.6 % (sd 2.3 %) and 17.8 % (sd 0.8 %), respectively. Mean H (expected average heterozygosity) was 5.9 % (sd 1.3 %) in the former and 5.9 % (sd 1.0 %) in the latter. In both species, P- and H-values in the Bulgarian, Slovenian, and Slovakian populations were among the highest as yet detected in these species. According to genetic distances and the exclusive occurrence of rare alleles the Bulgarian red deer represents a subspecies different from Central European *Cervus elaphus hippelaphus*. The wild boars were polymorphic at 11.6 % (sd 2.8 %) of their loci and had a mean H of 2.8 % (sd 0.5 %). Genetic distances revealed some distinctness of the population living in the Rila-Rodopi mountains from Central European *Sus scrofa scrofa*. Levels of migration (Nm) among local populations of all three species were very similar.

Introduction

The red deer (*Cervus elaphus*), the roe deer (*Capreolus capreolus*), and the wild boar (*Sus scrofa*) are among the most widely distributed European ungulate species (see Trense 1989). In all of them genetic diversity within and among populations has already been investigated by means of protein electrophoresis by several laboratories. Nevertheless, the studies conducted so far covered only a comparatively narrow part of the populations of each species and no attempts have been made to examine more than one species in a particular area. Considering only data which are to some extent comparable as to the number and composition of loci investigated, the red deer has been studied more extensively in southern Sweden (Gyllensten et al. 1983), in Scotland (Gyllensten et al. 1983; Dratch and Gyllensten 1985), in eastern France (Hartl et al. 1990a, 1991a), and in Hungary (Hartl et al. 1990a). In contrast, the roe deer has been screened almost exclusively in the Alpine area (Hartl et al. 1991b), and data on free-ranging wild boars are available only from Italy (Randi et al. 1989, 1992) and Bulgaria (Randi et al. 1992).

In the present study we examined genetic diversity within and among populations of red deer, roe deer, and wild boar in Bulgaria. The latter region is of particular population genetic interest, as there is considerable variation in elevation and ecological conditions (field vs. forest biotopes) within a narrow area. Furthermore, all species exhibit some morphological differences, suggesting the occurrence of two subspecies in wild boars (Markov 1954), a well defined field and forest ecotype in the roe deer (Markov et al. in prep.) and also some distinctness between red deer from the central part of the Balkan and the northeastern lowlands (Markov 1992a). For comparison with Central European

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5806-0352 $ 02.50/0

populations of the three species, samples from France, Germany, Austria, Slovakia, and Slovenia were screened additionally. Thereby it was attempted to obtain specimens from at least two species per sampling area.

Material and methods

Liver, kidney and heart of 75 red deer, 121 roe deer and 155 wild boars from various sampling sites (3 in the red deer, 5 in the roe deer, and 8 in the wild boar) in Bulgaria (Fig. 1) were collected during two hunting seasons (1990, 1991). Although being available in different numbers, in all species the samples cover populations from both field and forest/mountain biotopes. The habitat of sampling sites R3, r4, W1, W2, W3 and W8 consists of continuous mountaneous forests, that of R1, R2, r1, r2, W4, W6, W7 of large agricultural areas with small forest patches, and that of r3, r5, and W5 represents a transition between both extremes (Fig. 1).

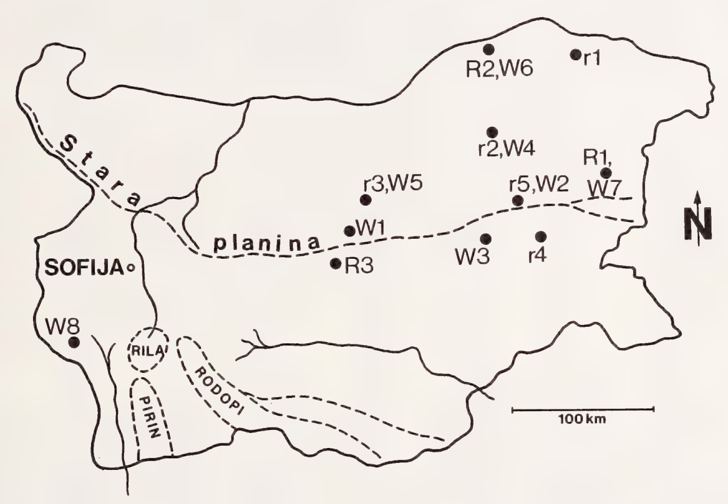


Fig. 1. Distribution of sampling sites of Bulgarian red deer (R1–R3), roe deer (r1–r5), and wild boars (W1–W8). Samples from field habitats (areas with extensive agriculture—: R1, R2, r1, r2, W4, W6, W7; from montaneous forest habitats: R3, r4, W1, W2, W3, W8; from transitional habitats: r3, r5, W5. Dashed lines: main crest of the Balkan (Stara planina), and mountains in southwestern Bulgaria

In addition, samples from the following populations of other parts of Europe were collected: Grosuplje (Gr – SLO, 19 roe deer), Sitno, Polana (Si, Po – ČSFR, 16 roe and 57 red deer), Eisenstadt (Ei – enclosure in southeastern Austria – comp. Hartl and Csaikl 1987; Hartl 1991, 27 wild boars, culled in 1990), Achenkirch (Ak – western Austria, 35 roe deer, 46 red deer) Eberbach (Eb – near Heidelberg, Germany, 16 wild boars), and the Northern Vosges (NV – France, 27 wild boars, 36 roe deer, data on red deer were taken from Hartl et al. 1991a).

Preparation of tissue extracts, horizontal starch gel electrophoresis and enzyme specific staining procedures were performed as described previously (Hartl and Höger 1986; Grillitsch et al. 1992). The following 33 isozyme systems were screened (abbreviation, E.C. number and tissues are given in parentheses – L = liver, K = kidney, H = heart): α-glycerophosphate dehydrogenase(GDC, E.C. 1.1.1.8, L), sorbitol dehydrogenase (SDH, E.C. 1.1.1.14, L), lactate dehydrogenase (LDH, E.C. 1.1.1.27, K), malate dehydrogenase (MDH, E.C. 1.1.1.37, K), malic enzyme (ME, E.C. 1.1.1.40, K), isocitrate dehydrogenase (IDH, E.C. 1.1.1.42, K), 6-phosphogluconate dehydrogenase (PGD, E.C. 1.1.1.44, K), glucose dehydrogenase (GDH, E.C. 1.1.1.47, L), glucose-6-phosphate dehydrogenase (GPD, E.C. 1.1.1.49, K), xanthine dehydrogenase (XDH, E.C. 1.2.3.2, L), glutamate dehydrogenase (GLUD, E.C. 1.4.1.3, L), NADH-diaphorase (DIA, E.C. 1.6.2.2, L, K), catalase (CAT, E.C. 1.11.1.6, K), superoxide dismutase (SOD, E.C. 1.15.1.1, K), purine nucleoside phosphorylase (NP, E.C. 2.4.2.1, K), aspartate aminotransferase (AAT, E.C. 2.6.1.1, K), hexokinase (HK, E.C. 2.7.1.1, K, H), pyruvate kinase (PK, E.C. 2.7.1.40, H), creatine kinase (CK, E.C. 2.7.3.2, K, H), adenylate kinase (AK, E.C. 2.7.4.3, K, H), phosphoglucomutase (PGM, E.C.

2.7.5.1, K), esterases (ES, E.C. 3.1.1.1, K), acid phosphatase (ACP, E.C. 3.1.3.2, K), fructose-1,6-diphosphatase (FDP, E.C. 3.1.3.11, K), β-galactosidase (β-GAL, E.C. 3.2.1.23, L), peptidases (PEP, E.C. 3.4.11, K), aminoacylase-1 (ACY-1, E.C. 3.5.1.14, K), adenosine deaminase (ADA, E.C. 3.5.4.4, L, K), aldolase (ALDO, E.C. 4.1.2.13, H), fumarate hydratase (FH, E.C. 4.2.1.2, L), aconitase (ACO, E.C. 4.2.1.3, K), mannosephosphate isomerase (MPI, E.C. 5.3.1.8, K), and glucosephosphate isomerase (GPI, E.C. 5.3.1.9, K).

The interpretation of electrophoretic band-patterns followed the principles outlined by Harris and Hopkinson (1976) and Harris (1980). Alleles were designated according to the relative electrophoretic mobility of the corresponding allozymes. In wild boars, at each polymorphic locus the most common allozyme in the Austrian population was designated "100". In the red deer and the roe deer, most of the alleles were already defined in Hartl and Reimoser (1988) and Hartl et al. (1990a, 1991a, b). The proportion of polymorphic loci (P, 99 per cent criterion), expected (H) and observed (H_o) average heterozygosity were calculated according to Ayala (1982). Genetic distances were calculated according to Nei (1972, 1978). Dendrograms were constructed by various methods reviewed in Hartl et al. (1990b) using the PHYLIP-programme package of Felsenstein (1985), the stability of clusters was examined by means of the jackknife and bootstrap method as described in the same paper. In cases where unique alleles occurred in one or the other sample, the theoretical amount of gene flow among populations was estimated using Slatkin's (1985) concept of 'private alleles' [$\bar{p}(1)$]. Since only few private alleles occurred, the conditional average frequency [$\bar{p}(i)$] for all alleles

Table 1. **Allele frequencies and genetic variation in red deer**

Locus	Allele	R1 (28)	R2 (13)	R3 (34)	Po (28)	Si (29)	Ak (46)	NV (233)
Me-1	100	0.714	0.833	0.647	0.700	0.938	0.851	0.983
	125	0.286	0.167	0.353	0.280	0.031	0.096	0.004
	90	0.0	0.0	0.0	0.020	0.031	0.053	0.013
Me-2	100	0.413	0.458	0.371	0.440*	0.625	0.707	0.635
	110	0.587	0.542	0.629	0.560	0.375	0.293	0.365
Idh-2	100	0.768	0.792	0.794	0.518*	0.655	0.415	0.423
	125	0.232	0.208	0.206	0.482	0.345	0.585	0.543
	112	0.0	0.0	0.0	0.0	0.0	0.0	0.034
Sod-2	−100	0.821	0.955	0.853	0.929	0.914	0.925	0.983
	−200	0.179	0.045	0.147	0.071	0.086	0.075	0.017
Pgm-2	100	0.740	0.875	0.677	0.964	0.983	0.957	0.974
	94	0.056	0.0	0.0	0.0	0.0	0.0	0.0
	89	0.148	0.125	0.226	0.036	0.017	0.011	0.026
	79	0.056	0.0	0.097	0.0	0.0	0.032	0.0
Acp-1	100	0.685*	0.542	0.885	0.607*	0.603	0.223	0.773
	300	0.315	0.458	0.115	0.393	0.397	0.777	0.227
Acp-2	100	0.423	0.292	0.307	0.185	0.034	0.478*	0.452
	85	0.269	0.416	0.597	0.815	0.966	0.522	0.548
	73	0.308	0.292	0.096	0.0	0.0	0.0	0.0
Mpi	100	0.964	0.962	0.868	1.0	1.0	0.862	1.0
	132	0.018	0.038	0.014	0.0	0.0	0.138	0.0
	70	0.018	0.0	0.118	0.0	0.0	0.0	0.0
Gpi-1	−100	0.982	0.923	0.971	1.0	1.0	1.0	1.0
	60	0.018	0.077	0.029	0.0	0.0	0.0	0.0
	P	0.209	0.209	0.209	0.163	0.163	0.186	0.163
	H	0.073	0.065	0.070	0.055	0.040	0.066	0.045
	H_o	0.073	0.066	0.072	0.037	0.036	0.065	0.043

R1–R3 = Bulgaria, Po = Polana (ČSFR), Si = Sitno (ČSFR), Ak = Achenkirch (A), NV = Northern Vosges (F). Sample sizes are given in parentheses. P = proportion of polymorphic loci (99 % criterion), H (H_o) = expected (observed) average heterozygosity. P, H, and H_o are calculated over 43 loci.
* observed genotypes deviated significantly from Hardy-Weinberg equilibrium.

was plotted against i/d, where i is the number of samples containing a particular allele and d is the total number of samples studied (SLATKIN 1981). This method does not permit a direct estimation of Nm, but gives an overall impression of the distribution of alleles among populations in relation to their frequencies. In the case of undisturbed migration, the number of samples in which an allele is present should monotonously increase together with an increase of the average frequency of the respective allele. Furthermore, G-statistics (NEI 1975) were used to assess relative differentiation among populations and also to estimate Nm from F_{ST} (in a broader sense) as outlined by SLATKIN and BARTON (1989).

Results

In order to obtain data fully comparable to those reported in previous studies (comp. HARTL et al. 1991a, b), not all isozymes were investigated in each species. In the red deer 43 presumptive structural loci were scored, 9 of which were polymorphic: Me-1, Me-2, Idh-2, Sod-2, Pgm-2, Acp-1, Acp-2, Mpi, and Gpi-1. Whereas all these loci were already found polymorphic by HARTL et al. (1990a, 1991a), some novel alleles were detected: Pgm-2^{94}, Acp-2^{73}, and Mpi^{70}. Allele frequencies in the various samples and indices of genetic variation are given in table 1. With the remarkable exception of Polana, where a significant deficiency of heterozygotes was deteced at three loci (Me-2, Idh-2, Acp-1), in the other samples genotypes at (almost) all polymorphic loci were in Hardy-Weinberg equilibrium. Calculated over the Bulgarian samples, mean P = 0.209 (sd. 0), mean H = 0.069 (sd. 0.004), G_{ST} = 0.038, Nm (calculated from G_{ST} – I) = 6.33, Nm (calculated from $\bar{p}(1)$ – II) = 2.40, and mean NEI's (1978) D = 0.0023 (sd. 0.0021). Calculated over all samples, mean P = 0.186 (sd. 0.023), mean H = 0.059 (sd. 0.013), G_{ST} = 0.096, Nm (I) = 2.35, Nm (II) = 1.58, and mean D = 0.0076 (sd. 0.0044). Genetic relationships among populations are shown in figure 2.

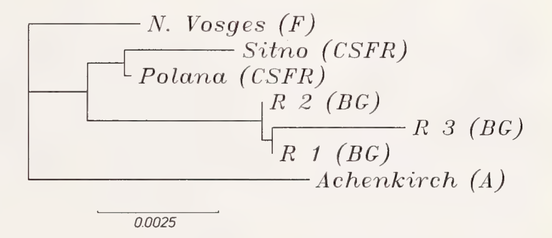


Fig. 2. Unrooted dendrogram, showing genetic relationships in red deer (NEI's 1978 D/FITCH-MARGOLIASH tree). A rooted dendrogram (NEI's 1978 D/UPGMA) was topologically identical and stable both with respect to sample sizes (bootstrap) and the composition of loci chosen (jackknife)

In the roe deer 8 out of 40 loci were polymorphic: Dia-2, Ak-1, Pgm-1, Pgm-2, Acp-1, Pep-2, Mpi, and Gpi-1. All loci were previously found polymorphic in this species (HARTL and REIMOSER 1988; HARTL et al. 1991b), but a novel allele, Pep-2^{120}, occurred exclusively in Bulgaria and Slovenia. Allele frequencies and indices of genetic variation are given in table 2. Calculated over the Bulgarian samples, mean P = 0.175 (sd. 0), mean H = 0.065 (sd. 0.003), G_{ST} = 0.044, Nm(I) = 5.43, and mean D = 0.0006 (sd. 0.0005). Calculated over all samples, mean P = 0.178 (sd. 0.008), mean H = 0.059 (sd. 0.010), G_{ST} = 0.064, Nm(I) = 3.69, Nm(II) = 37.38, and mean D = 0.0025 (sd. 0.0021). Genetic relationships among populations are shown in figure 3.

In wild boars 40 loci were examined. Nine of them were polymorphic: Me-1, Mdh-2, Dia, Pgm-2, Pgm-3, Pep-1, Acy-1, Ada-2, Gpi-1 (some of these polymorphisms were already described in Austrian wild boars by HARTL and CSAIKL 1987). Allele frequencies and indices of genetic variation are given in table 3. The following 31 loci were monomorphic: Gdc, Sdh, Ldh-1, -2, Mdh-1, Me-2, Idh-1, -2, Pgd, Gpd, Xdh, Glud, Cat, Sod-1, -2, Np, Aat-1, -2, Hk, Ck-2, Pgm-1, Acp-1, -2, Fdp, β-Gal, Pep-2, Fh, Aco-1, -2, Mpi,

Table 2. **Allele frequencies and genetic variation in roe deer**

Locus	Allele	Sample r1 (33)	r2 (21)	r3 (27)	r4 (23)	r5 (17)	Gr (19)	Si (16)	Ak (35)	NV (36)
Dia-2	100	0.939	0.976	0.963	0.913	0.941	0.842	0.969	0.986	0.972
	118	0.061	0.024	0.037	0.087	0.059	0.158	0.031	0.014	0.028
Ak-1	100	0.258*	0.309*	0.315	0.130	0.294	0.237	0.313	0.143	0.167
	250	0.742	0.691	0.685	0.870	0.706	0.763	0.687	0.857	0.833
Pgm-1	100	0.818	0.810	0.796	0.804	0.853	0.947	0.969	0.886	0.986
	−16	0.182	0.190	0.204	0.196	0.147	0.053	0.031	0.114	0.014
Pgm-2	100	0.750	0.790*	0.717*	0.658	0.546	0.605	0.500	0.714	0.615
	113	0.025	0.026	0.087	0.105	0.272	0.0	0.031	0.200	0.071
	70	0.225	0.184	0.196	0.237	0.182	0.395	0.469	0.086	0.314
Acp-1	100	0.685	0.474	0.546	0.650	0.567*	0.658	0.750	0.912	0.871
	200	0.315	0.526	0.454	0.350	0.433	0.342	0.250	0.088	0.129
Pep-2	100	0.267	0.306	0.282	0.238*	0.235	0.286	0.400	0.400	0.560
	120	0.167	0.027	0.109	0.0	0.118	0.107	0.0	0.0	0.0
	115	0.483	0.417	0.370	0.452	0.500	0.321	0.433	0.557	0.440
	107	0.083	0.250	0.239	0.310	0.147	0.286	0.167	0.043	0.0
Mpi	100	0.879	0.738	0.889	0.717	0.853	0.947	0.875	0.900	0.972
	120	0.121	0.262	0.111	0.283	0.147	0.053	0.125	0.100	0.028
Gpi	100	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.986	1.0
	300	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.014	0.0
	P	0.175	0.175	0.175	0.175	0.175	0.175	0.175	0.200	0.175
	H	0.062	0.067	0.064	0.065	0.069	0.062	0.057	0.045	0.041
	H_o	0.063	0.065	0.065	0.058	0.057	0.059	0.056	0.045	0.042

r1–r5 = Bulgaria, Gr = Grosuplje (SL), Si = Sitno (ČSFR), Ak = Achenkirch (A), NV = Northern Vosges (F). Sample sizes are given in parentheses. P = proportion of polymorphic loci (99 % criterion), H (H_o) = expected (observed) average heterozygosity. P, H, and H_o are calculated over 40 loci.
* observed genotypes deviated significantly from Hardy-Weinberg equilibrium.

and Gpi-2. Calculated over the Bulgarian samples, mean P = 0.122 (sd. 0.028), mean H = 0.029 (sd. 0.006), G_{ST} = 0.094, Nm(I) = 2.41, and mean D = 0.0062 (sd. 0.0217). Calculated over all samples, mean P = 0.116 (sd. 0.028), mean H = 0.028 (sd. 0.005), G_{ST} = 0.125, Nm(I) = 1.75, Nm(II) = 27.73, and mean D = 0.0032 (sd. 0.0029). Genetic relationships among populations are shown in figures 4 and 5.

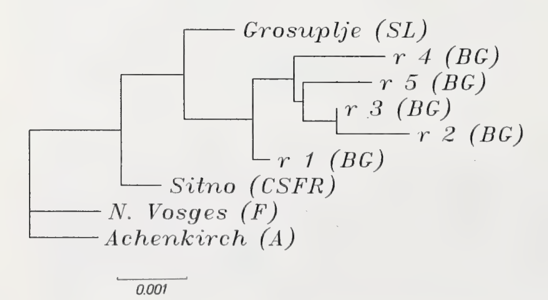


Fig. 3. Unrooted dendrogram, showing genetic relationships in roe deer (Fitch-Margoliash tree, since negative distances are not allowed Nei's 1972 D was used). A rooted dendrogram, (Nei's 1978 D/UPGMA) was topologically identical and stable both with respect to sample sizes (bootstrap) and the composition of loci chosen (jackknife)

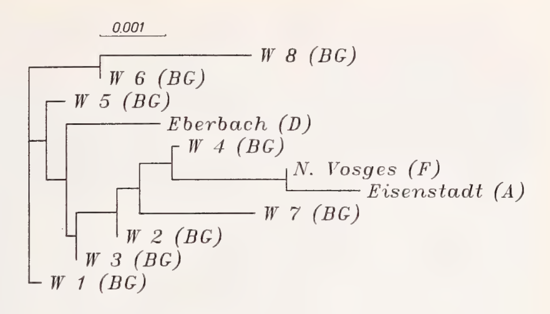


Fig. 4. Unrooted dendrogram, showing genetic relationships in wild boars (FITCH-MARGOLIASH tree, since negative distances are not allowed NEI's 1972 D was used)

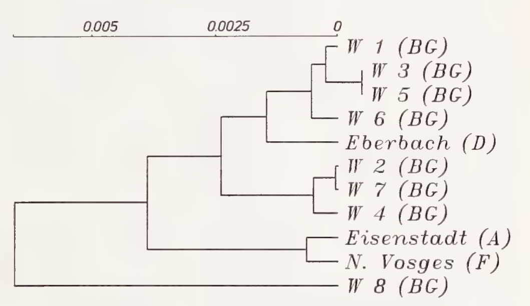


Fig. 5. Rooted dendrogram, showing genetic relationships in wild boars (NEI's 1978 D/UPGMA). The dendrogram was topologically unstable with respect to sample sizes (bootstrap), but stable with respect to the composition of loci chosen (jackknife)

Discussion

Red deer

Both with respect to the proportion of polymorphic loci and average heterozygosity, biochemical-genetic variation in the Bulgarian red deer is higher than in any other European population examined so far (comp. HARTL et al. 1990a, 1991a). Since novel alleles were detected and relative as well as absolute genetic differentiation were considerably smaller among only Bulgarian than among all samples, our data suggest that the red deer in that area is different from Central European *Cervus elaphus hippelaphus*. Genetic distances (Fig. 2) from French (NV), Austrian (Ak) or Czechoslovakian (Si) populations are of a magnitude described previously for other European subspecies of *Cervus elaphus* by GYLLENSTEN et al. (1983).

Red deer in Slovakia was extinct at the beginning of the 19th century and restocked in the Polana area – among others – with animals representing *C. e. carpathicus*. In our data, there is a deficiency of heterozygotes at several loci, possibly indicating a Wahlund effect (Tab. 1). Since there appear to be no geographical barriers within this area, the latter may be due to the formation of local demes as it has been discussed by SCHREIBER et al. (1992). Also the Austrian population (Ak) may contain not only autochthonous red deer, which is indicated by the comparatively large distance from all other populations studied (Fig. 2) and the presence of an MPI-polymorphism, lacking in all pure populations of Central European red deer examined so far (comp. Tab. 1, and GYLLENSTEN et al. 1983; HARTL et al. 1990a, 1991a), but being present in *C. e. scoticus* (PEMBERTON et al. 1988) and *C. e. canadensis* (DRATCH and GYLLENSTEN 1985). Attempts to introduce animals from the latter subspecies in Bavaria have been reported by BENINDE (1937).

Roe deer

Genetic variability in Bulgarian, Slovenian and Slovakian roe deer is high when compared to that of populations of Austria, Switzerland, France and Hungary (Tab. 2, and HARTL et

al. 1991b). This is due to the ubiquitous occurrence of many variant alleles showing only a scattered distribution in the populations examined by HARTL et al. (1991b) rather than to the presence of new polymorphisms. This result corresponds to the extremely low D- and G_{ST}-values within Bulgaria, suggesting the absence of any factors disturbing gene flow within the study area. Indeed, Nm within Bulgaria is the highest yet detected in this species (see HARTL et al. 1991b). The considerable difference between Nm as estimated from G_{ST} or from $\bar{p}(1)$ in the present study may be the result of sampling bias in the latter approach – only one private allele occurred). The close relationship among Bulgarian roe deer populations is in accordance with craniometric, somatometric and cytogenetic data (MARKOV and DOBRIJANOV 1985; MARKOV et al. 1991a, b).

As an adaptation to increasing deforestation, in the roe deer the existence of a distinct 'field ecotype' has been postulated by PIELOWSKI (1970), which differs from the classical 'forest ecotype' in various non-metric morphological, biochemical, physiological, and behavioural characteristics (e.g. PIELOWSKI 1977; MAJEWSKA et al. 1982; MARKOWSKI and MARKOWSKA 1988; KURT 1991). In our data, the pure representatives of both 'ecotypes' (r1, r4) did not show a genetic distance higher than typical for local populations (Fig. 3). This suggests that the 'field ecotype' reflects the adaptive potential of the species rather than a particular genetic integrity, whereby roe deer living in transitional habitats obviously play an important role in maintaining the gene flow between both extreme types (Figs. 1, 3).

Except for the Hungarian roe deer (HARTL et al. 1991b), overall genetic distances among the populations studied so far do not suggest the presence of different subspecies in Europe. HARTL et al. (1991b) proposed that the large average genetic distance (D = 0.0112) of the Hungarian roe deer from Austrian and Swiss populations may be the result of the completely fenced boarder existing between Austria and both Hungary and Czechoslovakia from the late 1940s to the late 1980s. Since the D-value between the Slovakian and the Austrian or the French roe deer is quite small (Fig. 3) this hypothesis is not supported by the present study.

Wild boars

In wild boars, genetic variation in the Bulgarian samples is not remarkably different from that in the other areas studied (Tab. 3). RANDI et al. (1992) found similar values of average heterozygosity, but a lower proportion of loci polymorphic which is probably due to a partially different set of proteins examined by these authors. In contrast to the roe and the red deer, the Bulgarian samples do not form a separate cluster (Figs. 4, 5), but are interspersed with Central European populations and, according to the bootstrap, all the clustes shown in figure 5 are not very stable. The Austrian population (Ei) is living in an enclosure, which was monitored by our laboratory from 1984 to 1990 by screening samples of an average size of 33 (sd. 9) specimens for allozyme polymorphism at the set of loci given in the present study every year. The population of about 300 individuals is annually reduced to one half both by battues and by selective elimination of 'weak' yearlings (for details see HARTL 1991). Average NEI's (1978) pairwise D among samples from seven consecutive years with 0.0039 (sd. 0.0031) is of the same magnitude as that among samples from the different locations examined in the present study (0.0032, sd. 0.0029). Although temporal changes of allele frequencies may be less extensive in free-ranging populations, this example shows that, probably due to the smaller number of polymorphic loci and the much smaller number of rare alleles, the pattern of geographical differentiation in wild boars may be less reliable than in the red or the roe deer. Nevertheless, population W8 is well separated from all other wild boars in the dendrogram (Fig. 4), which is in accordance with results based on 38 skull measurements (MARKOV 1992b). These data support the hypothesis, that the animals in the area of the Rila-Rodopi mountain massiv belong to an other subspecies than those from the eastern part of the

Table 3. **Allele frequencies and genetic variation in wild boars**

Locus	Allele	Sample										
		W1 (30)	W2 (15)	W3 (40)	W4 (25)	W5 (12)	W6 (15)	W7 (9)	W8 (9)	Ei (27)	Eb (16)	NV (27)
Me-1	100	0.966	1.0	1.0	0.905	0.950	1.0	0.889	1.0	0.982	1.0	0.907
	117	0.034	0.0	0.0	0.095	0.050	0.0	0.111	0.0	0.018	0.0	0.093
Mdh-2	100	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.982
	136	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.018
Dia	100	0.950	0.821	0.800	0.938	0.792	0.800	0.778	0.889	1.0	0.700	1.0
	132	0.050	0.179	0.200	0.062	0.208	0.200	0.222	0.111	0.0	0.300	0.0
Pgm-2	100	0.536	0.750	0.618	0.796	0.500	0.385	0.875	0.188	0.706	0.625	0.783
	113	0.464	0.250	0.382	0.204	0.500	0.615	0.125	0.812	0.294	0.375	0.217
Pgm-3	100	1.0	1.0	0.988	0.978	0.958	1.0	1.0	1.0	1.0	1.0	1.0
	110	0.0	0.0	0.012	0.022	0.042	0.0	0.0	0.0	0.0	0.0	0.0
Pep-1	100	0.933	0.900	0.938	0.980	0.875	0.933	1.0	1.0	0.667	1.0	0.769
	92	0.067	0.100	0.062	0.020	0.125	0.067	0.0	0.0	0.333	0.0	0.231
Acy-1	100	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.982
	123	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.018
Ada-2	100	0.867*	0.800	0.800*	0.875	0.750	0.923	0.667	0.778	1.0	1.0	1.0
	150	0.133	0.200	0.200	0.125	0.250	0.077	0.333	0.222	0.0	0.0	0.0
Gpi-1	−100	1.0	1.0	0.988	1.0	1.0	1.0	0.944	1.0	0.852	0.906	1.0
	−45	0.0	0.0	0.012	0.0	0.0	0.0	0.056	0.0	0.148	0.094	0.0
	P	0.125	0.100	0.150	0.150	0.150	0.100	0.125	0.075	0.100	0.075	0.125
	H	0.025	0.029	0.032	0.023	0.040	0.027	0.033	0.021	0.029	0.027	0.023
	H_o	0.025	0.022	0.033	0.018	0.042	0.027	0.037	0.014	0.026	0.025	0.023

W1–W8 = Bulgaria, Ei = Eisenstadt (A), Eb = Eberbach (D), NV = Northern Vosges (F). Sample sizes are given in parentheses. P = proportion of polymorphic loci (99 % criterion), H (H_o) = expected (observed) average heterozygosity. P, H, and H_o are calculated over 40 loci.
* observed genotypes deviated significantly from Hardy-Weinberg equilibrium.

country (Markov 1954). Considering the different distribution of sampling sites in both studies, our results are more or less in accordance with those of Randi et al. (1992). Like in the roe deer, the difference between Nm as estimated from G_{ST} or from $\bar{p}(1)$ may be the result of sampling bias in the latter (only two private alleles occurred).

Comparative aspects

In contrast to previous studies (Hartl and Reimoser 1988; Hartl et al. 1991b), mean P- and H-values were very similar between the red and the roe deer, which is probably the result of collecting samples from the same sites or at least from similar habitats, respectively. The number of populations in which an allele is present increases monotonously with its average frequency in all three species, which, together with the similar Nm (when calculated from G_{ST}), indicates a similar amount of migration in all three species. Only in the red deer there is an exception as to alleles occurring in four samples (Me-1^{90}, Mpi^{132} – Tab. 1), where the expected average frequency is much too low. This could possibly be the result of natural (Mpi^{132}, Pemberton et al. 1988) or artificial (Me-1^{90}, Hartl et al. 1991a) selection discriminating against these alleles.

In the roe and the red deer, the Bulgarian samples are well separated from the Central European populations and (as far as samples are available) are more closely related to those from Slovenia and Slovakia than to those from Austria or France. According to the

exclusive occurrence of rare alleles in both species (Tab. 1, 2) Bulgarian roe and red deer represent a distinct gene pool which should neither be contaminated by introductions of deer from abroad nor serve as a source for restocking in Central Europe. At least with regard to the population living in the Rila/Rodopi mountains this statement is valid also for wild boars.

Acknowledgements

The authors are indebted to Dr. A. Bidovec, to Dr. H. Herbold and to the local hunters in Bulgaria, Slovenia, Austria, and Slovakia for the collection of samples. The excellent technical assistance of Anita Haiden is gratefully acknowledged.

Zusammenfassung

Allozymdiversität innerhalb und zwischen Populationen dreier Ungulatenarten (Cervus elaphus, Capreolus capreolus, Sus scrofa) aus Südost- und Mitteleuropa

Mittels horizontaler Stärkegelelektrophorese wurde bei 75 Rothirschen, 121 Rehen und 155 Wildschweinen aus verschiedenen Regionen Bulgariens die genetische Variabilität und Differenzierung an 40–43 Genloci untersucht. Zum Vergleich mit mitteleuropäischen Populationen wurden weitere 103 Rothirsche, 106 Rehe und 70 Wildschweine aus Probengebieten in Slowenien, Österreich, der Slowakei und Frankreich herangezogen. Der durchschnittliche Polymorphiegrad (P, 99 % Kriterium) betrug beim Rothirsch 18,6 % (sd. 2,3 %) und beim Reh 17,8 % (sd. 0,8 %), die durchschnittliche Heterozygotierate betrug bei beiden Arten 5,9 % (sd. 1,3 % bzw. 1,0 %). Sowohl beim Rothirsch als auch beim Reh waren der Polymorphiegrad und die Heterozygotierate der bulgarischen, slowenischen und slowakischen Populationen höher als die meisten bisher beschriebenen P- und H-Werte. Die genetischen Distanzen zu anderen Beständen und das ausschließliche Vorkommen bestimmter Allele unterscheiden die bulgarischen Rothirschpopulationen auf dem (elektrophoretischen) Niveau einer Unterart vom mitteleuropäischen *Cervus elaphus hippelaphus*. Die Wildschweine waren im Durchschnitt an 11,6 % (sd. 2,8 %) der Loci polymorph und zeigten einen mittleren Heterozygotiegrad von 2,8 % (sd. 0,5 %). Nach den genetischen Distanzen unterscheidet sich die Population in den Rila-Rodopi-Bergen deutlich von der mitteleuropäischen Unterart *Sus scrofa scrofa*. Der Migrationsgrad (Nm) zwischen den Populationen war bei allen drei Arten sehr ähnlich.

References

Ayala, F. J. (1982): Population and Evolutionary Genetics: A Primer. Benjamin Cummings: Menlo Park, CA.

Beninde, J. (1937): Zur Naturgeschichte des Rothirsches. Reprint der Originalausgabe 1988. Hamburg, Berlin: Paul Parey.

Dratch, P.; Gyllensten, U. (1985): Genetic differentiation of red deer and North American elk (Wapiti). Biology of Deer Production, R. Soc. NZ. Bull. **22**, 37–40.

Felsenstein, J. (1985): Confidence limits on phylogenies: an approach using the bootstrap. Evolution **39**, 783–791.

Grillitsch, M.; Hartl, G. B.; Suchentrunk, F.; Willing, R. (1992): Allozyme evolution and the molecular clock in the Lagomorpha. Acta Theriologica **37**, 1–13.

Gyllensten, U.; Ryman, N.; Reuterwall, C.; Dratch, P. (1983): Genetic differentiation in four European subspecies of red deer (*Cervus elaphus* L.). Heredity **51**, 561–580.

Harris, H. (1980): The Principles of Human Biochemical Genetics. Amsterdam: Elsevier/North Holland.

Harris, H.; Hopkinson, D. A. (1976): Handbook of Enzyme Electrophoresis in Human Genetics. Amsterdam: Elsevier/North Holland.

Hartl, G. B. (1991): The influence of game management on allelic variation in large mammals of Central Europe. In: Genetics and Wildlife Conservation. Ed. by E. Randi and M. Spagnesi. Suppl. Ric. Biol. Sel. **18**, 95–108.

Hartl, G. B.; Csaikl, F. (1987): Genetic variability and differentiation in wild boars (*Sus scrofa ferus* L.): Comparison of isolated populations. J. Mammalogy **68**, 119–125.

Hartl, G. B.; Höger, H. (1986): Biochemical variation in purebred and crossbred strains of domestic rabbits (*Oryctolagus cuniculus* L.). Genetical Research, Camb. **48**, 27–34.

Hartl, G. B.; Lang, G.; Klein, F.; Willing, R. (1991a): Relationships between allozymes, heterozygosity and morphological characters in red deer (*Cervus elaphus*), and the influence of selective hunting on allele frequency distributions. Heredity **66**, 343–350.

Hartl, G. B.; Willing, R.; Lang, G.; Klein, F.; Köller, J. (1990a): Genetic variability and

differentiation in red deer (*Cervus elaphus* L.) of Central Europe. Genetics, Selection, Evolution **22**, 289–306.

HARTL, G. B.; WILLING, R.; SUCHENTRUNK, F. (1990b): On the biochemical systematics of selected mammalian taxa: empirical comparison of qualitative and quantitative approaches in the evaluation of protein electrophoretic data. Z. zool. Syst. Evolut.-forsch. **28**, 191–216.

HARTL, G. B.; REIMOSER, F. (1988): Biochemical variation in roe deer (*Capreolus capreolus* L.): are r-strategists among deer genetically less variable than K-strategists? Heredity **60**, 221–227.

HARTL, G. B.; REIMOSER, F.; WILLING, R.; KÖLLER, J. (1991b): Genetic variability and differentiation in roe deer (*Capreolus capreolus* L.) of Central Europe. Genetics, Selection, Evolution **23**, 281–299.

KURT, F. (1991): Das Reh in der Kulturlandschaft. Sozialverhalten und Ökologie eines Anpassers. Hamburg, Berlin: Paul Parey.

MAJEWSKA, B.; PIELOWSKI, Z.; LABUDZKI, L. (1982): The level of some energy metabolism indices in forest and field populations of roe deer. Acta Theriologica **27**, 471–477.

MARKOV, G. (1954): [On the systematics of the wild boar in Bulgaria]. Bull. de'l Institut Zool. de'l Acad. Bul. Sci., Sofia **3**, 221–223, (in Bulgarian with Englisch summary).

— (1992a): Craniometric study of Bulgarian red deer populations. Acta zool. bul. (in press).

— (1992b): Craniometric variability of wild boar (*Sus scrofa*) in Bulgaria. Forest Science (in press).

MARKOV, G.; DOBRIJANOV, D. (1985): [Caryotaxonomic investigation of roe deer (*Capreolus capreolus* L. 1758) in Bulgaria]. Acta zool. bul. **28**, 3–9 (in Bulgarian with Englisch summary).

MARKOV, G.; GERASIMOV, S.; PETROV, M.; NIKOLOV, H. (1991a): [Somatometric investigation of roe deer (*Capreolus capreolus* L. 1758) in Bulgaria]. Forest Science **3**, 52–56, (in Bulgarian with English summary).

— — — — (1991b): Craniometric characteristics of roe deer (*Capreolus capreolus* L. 1758) in Bulgaria]. Forest Science **4**, 84–90, (in Bulgarian with English summary).

MARKOWSKI, J.; MARKOWSKA, M. (1988): Non-metrical variation in three populations of roe deer. Acta Theriologica **33**, 519–536.

NEI, M. (1972): Genetic distance between populations. Amer. Naturalist **106**, 283–292.

— (1975): Molecular Population Genetics and Evolution. Amsterdam: Elsevier/North Holland.

— (1978): Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics **89**, 583–590.

PEMBERTON, J. M.; ALBON, S. D.; GUINNESS, F. E.; CLUTTON-BROCK, T. H.; BERRY, R. J. (1988): Genetic variation and juvenile survival in red deer. Evolution **42**, 921–934.

PIELOWSKI, Z. (1970): Sarna. Monografia przyrodniczo-lowiecka. Warszawa: Panstw. Wyd. Roln. i. Lesne., 1–220.

— (1977): Das Feldreh. Wild der Zukunft in der Agrarlandschaft. Beitr. Jagd- und Wildforsch. **10**, 193–200.

RANDI, E.; APOLLONIO, M.; TOSO, S. (1989): The systematics of some Italian populations of wild boar (*Sus scrofa* L.): A craniometric and electrophoretic analysis. Z. Säugetierkunde **54**, 40–56.

RANDI, E.; MASSEI, G.; GENOV, P. (1992): Allozyme variability in Bulgarian wild boar populations. Acta Theriologica **37**, 271–278.

SCHREIBER, A.; KLEIN, F.; LANG, G. (1992): Deficiency of heterozygotes at the transferrin locus in an autochthonous population of Central European red deer. In: Ongules/Ungulates 91. Ed. by F. SPITZ; G. JANEAU; G. GONZALEZ; S. AULAGNIER. Paris, Toulouse: S.F.E.P.M. – I.R.G.M. 117–122.

SLATKIN, M. (1981): Estimating levels of gene flow in natural populations. Genetics **99**, 323–335.

— (1985): Rare alleles as indicators of gene flow. Evolution **39**, 53–65.

SLATKIN, M.; BARTON, N. H. (1989): A comparison of three indirect methods for estimating average levels of gene flow. Evolution **43**, 1349–1368.

TRENSE, W. (1989): The Big Game of the World. Hamburg, Berlin: Paul Parey.

Authors' addresses: Dr. GÜNTHER B. HARTL, Mag. ANGELIKA RUBIN and Dipl. Ing. RUDOLF WILLING, Forschungsinstitut für Wildtierkunde und Ökologie der Veterinärmedizinischen Universität Wien, Savoyenstraße 1, A-1160 Vienna, Austria; Dr. GEORGY MARKOV, Institute of Zoology, Bulgarian Academy of Science, 1, Tsar Osvoboditel bul., 1000 Sofia, Bulgaria; Ing. SLAVOMIR FINDO, Forest Research Institue, ul. T. g. Masaryka 22, 960 92 Zvolen, Slovakia; Dr. GERARD LANG, 26a, Rue Principale, F-67240 Gries, France

Z. Säugetierkunde 58 (1993) 362–367

ISSN 0044-3468

Thermoregulation and metabolic acclimation in the Natal mole-rat (*Cryptomys hottentotus natalensis*) (Rodentia: Bathyergidae)

By N. C. Bennett, P. J. Taylor, and G. H. Aguilar

Department of Zoology, University of Cape Town, Cape Town and Durban Natural Science Museum, Durban, R.S.A.

Receipt of Ms. 30. 10. 1992
Acceptance of Ms. 20. 12. 1992

Abstract

The social Natal mole-rat *Cryptomys hottentotus natalensis* has a mean (± S.D.) resting metabolic rate (RMR) when newly captured of 1.03 ± 0.25 cm^3 O_2 g^{-1} h^{-1} (n = 7) at an ambient temperature (Ta) of 30 °C, within the thermoneutral zone (TNZ) of 30–31.5 °C. Two months after maintenance in the laboratory at 26 °C, the RMR of the same animals showed a concomitant drop in value of 20 % at 30 °C (TNZ) to a mean of 0.80 ± 0.12 cm^3 O_2 g^{-1} h^{-1} (n = 14), indicating that laboratory acclimation had occurred.

The body temperature of the mole-rat is low 33.4 ± 0.83 (n = 36) and remains stable at Ta's from 10–30 °C. Above 31.5 °C, Tb increases albeit slightly to 35.7 ± 0.51 °C (n = 24). The conductance is high 0.13 ± 0.03 cm^3 O_2 g^{-1} h^{-1} $°C^{-1}$ (n = 24) at the lower limit of thermoneutrality. The mean RMR at 18 °C (the lowest Ta tested) was 1.83 ± 0.46 cm^3 O_2 g^{-1} h^{-1}, which is 2.2 times that of the RMR in the TNZ.

The nest (where mole-rats rest for up to 80 % of the day) is the focal point of the burrow system. The selection for *C. h. natalensis* to acclimate within its TNZ may relate to seasonal fluctuations in the temperature occurring in the shallow nest, resulting in seasonal acclimatisation in RMR.

Introduction

The Natal mole-rat (*Cryptomys hottentotus natalensis*) is a semi-social subterranean rodent occurring in pairs or small family groups comprising as many as six individuals (Hickman 1982). A reproductive division of labour similar to that of other species and subspecies of the genus occurs (Bennett 1988; Bennett and Jarvis 1988; Bennett 1989, 1990). In each burrow system only one female will reproduce.

The Natal mole-rat excavates extensive tunnel systems which can exceed 340 m in total length (Hickman 1979). The burrow systems are sealed from the surface and consist of numerous shallow long sub-surface foraging tunnels approximately 20 cm deep and a deeper (approximately 30 cm) central nest area slightly more protected from predators and temperature extremes (Hickman 1979; Bennett et al. 1988). *Cryptomys h. natalensis* rarely ventures onto the surface and therefore lives in a buffered thermal environment.

The systematics of the genus *Cryptomys* has been in a taxonomic disarray. Karyotypic differences in morphology involving pericentric inversions and allozyme fixations are evident between *C. h. natalensis* and *C. h. hottentotus* (Nevo et al. 1986, 1987). Indeed, Nevo et al. (1987) have suggested that the two subspecies deserve specific recognition. The size of the colonies are markedly different, with *C. h. hottentotus* occurring in colonies of up to 17 individuals (Rosenthal et al. 1992). This paper reports the RMR, TNZ, conductance and the ability to acclimate in the Natal mole-rat and compares the physiological similarities of *C. h. natalensis* with that of another species and subspecies of the genus *Cryptomys*.

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5806-0362 $ 02.50/0

Material and methods

Experimental animals

Seven *Cryptomys h. natalensis* (3 females and four males) were collected from Loteni, Natal (29° 32′ E, 29° 13′ S), Garden Castle, Natal (29° 16′ E, 29° 46′ S) and the Botanic Gardens, Durban, Natal (31° 0′ E, 29° 50′ S) in the Natal Province, South Africa. Body mass (M) of the individuals ranged from 60–182 g ($\bar{x}$ = 102, n = 7). The mole-rats were housed separately in plastic containers in a constant temperature room at 26 °C. Wood shavings and paper towelling were provided as nesting material. The mole-rats were fed on a variety of vegetables, supplemented weekly with a high protein Pronutro® cereal.

Experimental procedure

Air flow-rate was determined using a bubble flowmeter constructed of a modified burette containing soap water. The respirometer consisted of a cylindrical transparent Perspex chamber (800 cm^3) fitted with 6 mm diameter inlet and outlet ports. Temperatures were kept constant within the respirometer by placing it inside a small (0.11 m^3) temperature-controlled cabinet. A negative pressure flow-through system was used. Outside air was pulled through the respirometer, scrubbers (CO_2 trap of soda lime and water trap of colour-indicator silica gel) and oxygen analyser at a flow rate of 315–326 cm^3 min^{-1}.

The techniques of Bartholomew et al. (1985) and Lighton (1985) were used to measure $\dot{V}O_2$ with an Applied Electrochemistry S-3A two-channel oxygen analyser connected to a British Broadcasting Corporation microcomputer. This procedure records the voltage between the fractional concentrations of oxygen in the respiratory and calibration streams (Lovegrove 1987). $\dot{V}O_2$ expressed as a mass-specific rate was calculated according to the equation of Depocas and Hart (1957) as:

$$\dot{V}O_2 = \frac{(F_1O_2 - F_2O_2)\, V_2}{(1 - F_1O_2)}$$

where F_1O_2, is the O_2 fraction of the inlet ir and F_2O_2 the outlet air once the chamber was connected to the measuring circuit. $\dot{V}O_2$ is expressed as cm^3 O_2 g^{-1} h^{-1} and $\dot{V}_2$ is in cm^3 of air h^{-1}. Values were corrected to S.T.P. conditions.

The progress of each run was visually monitored on a visual display unit, and markers were placed on the trace to correspond with behavioural observations of resting made during the run. Each run was programmed to last 180 min, with data points being collected every 17 sec. The initial 30 min of the run was used to allow the animals to settle and consequently this section of the trace was not analysed.

A portion of the trace of approximately 20 min in length corresponding to the lowest stable oxygen consumption when the mole-rat was calm and completely at rest was integrated and calculated in cm^3 O_2 g^{-1} h^{-1} (S.T.P.) and presented as the mean ± S.D. for each respective Ta. However, at lower temperatures (18 and 21 °C) portions of trace of approximately 5–10 min in length were used because the mole-rats were reluctant to rest for longer periods of time.

The relationship of $\dot{V}O_2$ and Ta, when Ta was below the lower limit of thermoneutrality (T1) was analysed using a regression analysis for repeated measures (Sokal and Rohlf 1980). Conductance below T1 was calculated from individual measurements of $\dot{V}O_2$ using the formula Cm = $\dot{V}O_2$/(Tb-Ta) (McNab 1980) and presented as a mean ± S.D. in cm^3 O_2 g^{-1} h^{-1}.

Experiments were run between 08.00 h and 18.00 h to lessen the effect of any potential endogenous rhythms of metabolism. The animals were deprived of food 3 h prior to the measurement of metabolic rate in order to achieve a post-absorptive state and reduce the influence of specific dynamic action. Body (rectal) temperature (Tb) and ambient temperatures (Ta) were measured using copper-constantan thermocouples (4 mm diameter). For the rectal temperature measurements, the copper-constantan thermocouple was inserted 1.3 cm into the animal's rectum after the mole-rat had been left for 2 h at the required Ta in the temperature-controlled cabinet. To avoid undue stress at the upper and lower extremes of temperature, the mole-rats were only left in the cabinet for 1 h. Oxygen consumption was not measured below 18 °C, because the mole-rats invariably rested for too short a time period to get a meaningful $\dot{V}O_2$.

Results

The body temperature of *C. h. natalensis* remained stable at Ta's from 10 to 30 °C with a mean value of 33.4 ± 0.83 °C (n = 36). Above 31.5 °C (31.5–37 °C) Tb increased to 35.7 ± 0.51 °C (n = 34) (Fig. 1).

The mean RMR of newly captured *C. h. natalensis* was 1.03 ± 0.25 cm^3 O_2 g^{-1} h^{-1}

(n = 7) at 30 °C within the TNZ of 30–31.5 °C. Two months after maintenance in the laboratory at 26 °C, the RMR of the same animals showed a concomitant drop in value by 20 % at 30 °C (TNZ) to 0.80 ± 0.12 cm^3 O_2 g^{-1} h^{-1}, indicating that laboratory acclimation had resulted (Fig. 2). Below the lower limit of thermoneutrality the increase in metabolic rate is given by the equation y = 3.582 – 0.100X r^2 = 0.98 (model for more than one value

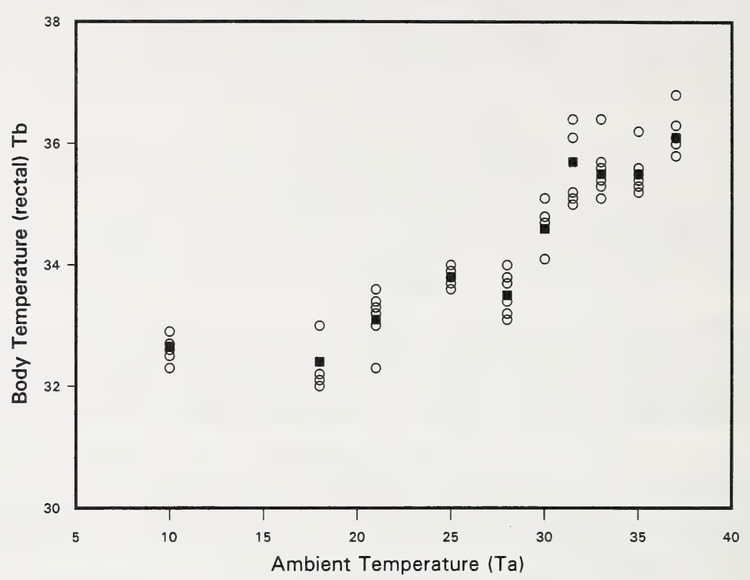


Fig. 1. Mean ■ and individual ○ body temperature (Tb) of seven Natal mole-rats, *Cryptomys hottentotus natalensis*, as a function of ambient temperature (Ta)

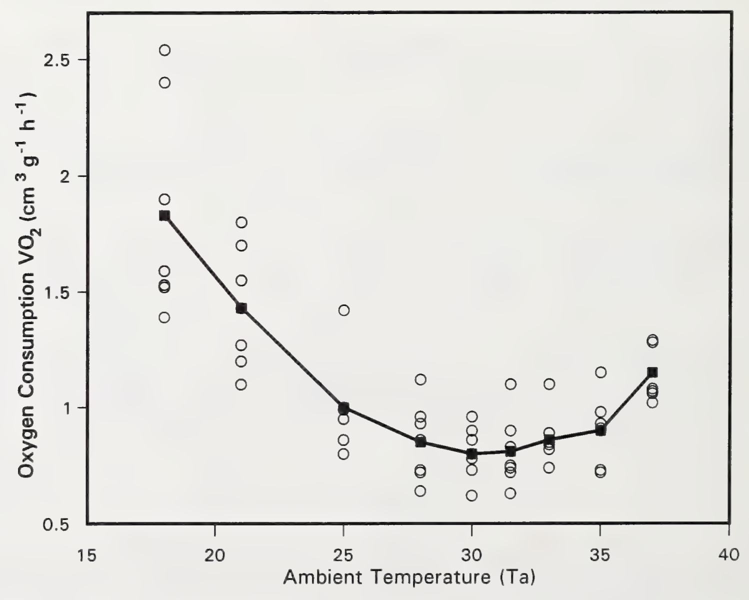


Fig. 2. Mean ■ and individual ○ oxygen consumption (cm^3 O_2 g^{-1} h^{-1}) of seven Natal mole-rats, *Cryptomys hottentotus natalensis*, as a function of ambient temperature (°C)

of y per value of x) (Sokal and Rohlf 1980). The conductance was high 0.13 ± 0.03 $cm^3\ O_2\ g^{-1}\ h^{-1}$ (n = 24) at the lower limit of thermoneutrality. The conductance of a Natal mole-rat of mean body mass 102 g assuming a RQ of 0.8 is 73.7 mW/°C.

The mean metabolic rate at 18 °C (the lowest Ta tested) was 1.83 ± 0.46 $cm^3\ O_2\ g^{-1}\ h^{-1}$, which is 2.2 times that of the RMR in the TNZ. The mole-rat was able to maintain its Tb below thermoneutrality showing that the increase in heat production was sufficient to offset the greater heat loss induced by lower ambient temperature.

Discussion

Subterranean rodents spend their lives underground in sealed tunnel-systems and rarely, if ever, come to the surface (Nevo 1979). Morphological and physiological specialisations of the mole-rat permit efficient excavation, foraging and locomotion in an underground labyrinth (Eloff 1958; Lovegrove 1987; Jarvis and Bennett 1990, 1991). Foraging galleries are shallow (ca 20 cm below ground) and the temperatures experienced in these burrows represent the extremes to which the animals are exposed in the natural environment.

The annual amplitude in temperature fluctuation is greatest at the soil surface, diminishing with increasing depth. Mean annual soil temperatures vary minimally at depths exceeding 0.6 m (Bennett et al. 1988). The mole-rats spend between 70–80 % of the 24 h day resting or sleeping in the nest (Bennett 1990), and temperatures experienced in this locality will greatly influence their daily energy expenditure (D.E.E.). The nest of *C. h. natalensis* is shallow ± 20–30 cm (Hickman 1979). The shallow nest of *C. h. natalensis* probably experiences a seasonal change in core temperature.

Physiologically, subterranean rodents show traits such as low body temperatures, low resting metabolic rates and high conductances (McNab 1979). The study animal exhibited physiological adaptations characteristic of subterranean bathyergids

Mean body mass, resting metabolic rate, body temperature and social status of bathyergid subterranean rodents

Species	Mean body mass (g)	RMR $cm^3\ g^{-1}\ h^{-1}$	Body temperature in TNZ (°C)	Social status	Habitat (degree of rainfall)	References
Heterocephalus glaber	39.5	0.64–1.00	32	social	semi-arid/arid	McNab (1979), Buffenstein and Yahav (1991)
Cryptomys h. darlingi	60	0.98	33	social	semi-arid	Bennett et al. (1992)
Cryptomys h. hottentotus (N. Cape)	75	0.9–1.3	34	social	semi-arid	Bennett et al. (1992)
Heliophobius argenteocinereus	88	0.85	35	solitary	mesic	McNab (1979)
Cryptomys h. hottentotus (Transvaal)	95	0.68	35.8	social	mesic	Haim and Fairall (1986)
Cryptomys h. natalensis	102	0.80–1.0	33.8	social	mesic	This study
Cryptomys damarensis	125	0.57–0.66	35	social	semi-arid/arid	Lovegrove (1986a), Bennett et al. (1992)
Georychus capensis	181	0.59	36.4	solitary	mesic	Lovegrove (1987)
Bathyergus janetta	406	0.53	34.8	solitary	semi-arid/arid	Lovegrove (1986b)
Bathyergus suillus	620	0.49	35	solitary	mesic	Lovegrove (1986b)

except that *C. h. natalensis* had a higher RMR than most of the solitary species of bathyergid rodent (Table). In contrast to previous reports on RMR's in bathyergids (LOVEGROVE 1986a, b, 1987) *C. h. natalensis* has a markedly higher RMR, most reminiscent of the RMRs recorded for the spalacids, geomyids (NEVO and SHKOLNIK 1974; BRADLEY et al. 1974) and the other social bathyergids (Table) (BENNETT et al. 1992; BUFFENSTEIN and YAHAV 1991).

Our work has shown that *C. h. natalensis* maintained in captivity (two months after capture) had a mean RMR (0.80 cm^3 O_2 g^{-1} h^{-1}) 20 % lower than when freshly (1.03 cm^3 O_2 g^{-1} h^{-1}) caught. Another subspecies of the genus *Cryptomys, C. h. hottentotus* similarly showed laboratory acclimation (BENNETT et al. 1992). The nest of *C. h. hottentotus* is of comparable depth (approximately 40 cm) and again probably experiences seasonal temperature changes. In contrast, the Damaraland mole-rat, *Cryptomys damarensis* does not show metabolic acclimation to laboratory conditions. This may be the direct result of the depth of the nest, which in this species is between 1.6–2.3 m in depth (BENNETT 1988).

A mole-rat utilizing a deep nest (where core temperature remains stable throughout the year) would thus have negligible selective pressures acting upon them to acclimate or seasonally acclimatise. The converse is true of dwellers of shallow nests, where there is seasonal fluctuation in nest core temperature and hence a selection to respond to these changes by adjusting the RMR. Afrotropical mole-rats occupying ecotopes which experience more equiable thermal regimes may respond in a different manner to laboratory acclimation. To date, mole-rats occurring in temperate climates with shallow nests appear to acclimate within the TNZ.

Acknowledgements

We are grateful to the University of Cape Town and Foundation for Research and Development for grants to one of us (N.C.B.) to conduct this research. We thank the Department of Nature Conservation for permits to collect the animals. Dr. WALTER LIEBRICH provided the German translation. KATE RICHARDSON provided invaluable support with caring for the animals in the field. GROVE ANNESLEY and R. NGUBANE also assisted with the care of the animals.

Zusammenfassung

Thermoregulation und metabolische Anpassung beim Hottentotten-Graumull (Cryptomys hottentotus natalensis) (Rodentia: Bathyergidae)

Frischfänge der sozial lebenden Graumulle haben innerhalb ihrer thermischen Neutralzone (TNZ) von 30–31,5 °C eine mittlere Ruhestoffwechselrate (RMR) von 1,03 ± 0,25 cm^3 O_2 g^{-1} h^{-1} (n = 7). Nach zwei Monaten Haltung im Labor (26 °C) fällt die RMR der gleichen Tiere um 20 % und erreicht einen mittleren Wert von 0,80 ± 0,12 cm^3 O_2 g^{-1} h^{-1} (n = 14). Dies zeigt, daß eine Anpassung an die Laborbedingungen erfolgt ist.

Die Körpertemperatur des Graumulls ist niedrig und beträgt im Mittel 33,4 ± 0,83 °C (n = 36); sie bleibt bei Umgebungstemperaturen von 10–30 °C stabil. Über 35 °C steigt sie auf 35,7 ± 0,51 °C an (n = 24). Die Wärmeleitfähigkeit (conductance) ist an der unteren Grenze der TNZ hoch (0,13 ± 0,03 cm^3 O_2 g^{-1} h^{-1} $°C^{-1}$; n = 24). Bei 18 °C (niedrigste getestete Temperatur) beträgt die mittlere RMR 1,83 ± 0,46 cm^3 O_2 g^{-1} h^{-1}; sie liegt damit 2,2mal höher als im Bereich der TNZ.

Das Nest, in dem sich Graumulle bis zu 80 % des Tages aufhalten, ist der Mittelpunkt des Höhlensystems. Die charakteristischen Eigenschaften und die Veränderungen des Nestmikroklimas (von der Tiefe abhängig) könnten wichtige Faktoren bei der Temperaturanpassung und der jahreszeitlichen Akklimatisation sein. Die Anpassung der RMR innerhalb der TNZ steht möglicherweise im Zusammenhang mit den Temperaturschwankungen in dem nahe der Oberfläche gelegenen Nest.

References

BARTHOLOMEW, G. A.; LIGHTON, J. R. B.; LOUW, G. N. (1985): Energetics of locomotion and patterns of respiration in tenebrionid beetles from the Namib desert. J. Comp. Physiol. **155**, 155–162.

BENNETT, N. C. (1988): The trend towards sociality in three species of southern African mole-rats (Bathyergidae): causes and consequences. Unpubl. Ph.D. diss. Univ. of Cape Town.

— (1989): The social structure and reproductive biology of the common mole-rat, *Cryptomys h. hottentotus*, and remarks on the trends in reproduction and sociality in the Family Bathyergidae. J. Zool. (London) **219**, 45–59.
— (1990a): Behaviour and social organisation in a colony of the Damaraland mole-rat *Cryptomys damarensis*. J. Zool. (London) **220**, 225–248.
— (1990b): The social season is underground: the mole-rats of southern Africa. African wildlife **44**, 299–301.
Bennett, N. C.; Clarke, B. C.; Jarvis, J. U. M. (1992): A comparison of metabolic acclimation in two species of social mole-rats (Rodentia, Bathyergidae) in southern Africa. J. Arid Environ. **22**, 189–198.
Bennett, N. C.; Jarvis, J. U. M. (1988): The social structure and reproductive biology of colonies of the mole-rat *Cryptomys damarensis* (Rodentia, Bathyergidae). J. Mammalogy **69**, 293–302.
Bennett, N. C.; Jarvis, J. U. M.; Cotterill, F. P. D. (1992): Poikilothermic traits and thermoregulation in the Afrotropical Mashona mole-rat (*Cryptomys hottentotus darlingi*). J. Zool. (London) (in press).
Bennett, N. C.; Jarvis, J. U. M.; Davies, K. C. (1988): Daily and seasonal temperatures in the burrows of African rodent moles. S. Afr. J. Zool. **23**, 189–195.
Bradley, W. G.; Millar, J. S.; Yousef, M. K. (1975): Thermoregulatory patterns in Pocket gophers. Physiol. Zool. **47**, 172–179.
Buffenstein, R.; Yahav, S. (1991): Is the naked mole-rat, *Heterocephalus glaber* a poikilothermic or poorly thermoregulatory endothermic mammal? J. Thermal. Biol. **16**, 227–232.
Depocas, F.; Hart, J. S. (1957): Use of the Pauling oxygen analyser for measurement of oxygen consumption of animals in open-circuit systems and in short-lag, closed-circuit apparatus. J. Applied Physiol. **10**, 388–392.
Eloff, G. (1958): The functional and structural degeneration of the eye of the South African rodent moles *Cryptomys bigalkei* and *Bathyergus maritimus*. S. Afr. J. Sci. **54**, 293–302.
Hickman, G. C. (1979): Burrow system structure of the bathyergid *Cryptomys hottentotus* in Natal, South Africa. Z. Säugetierkunde **44**, 153–162.
— (1982): Copulation of *Cryptomys hottentotus* (Bathyergidae), a fossorial rodent. Mammalia **46**, 293–297.
Jarvis, J. U. M.; Bennett, N. C. (1990): The evolutionary history, population biology and social structure of African mole-rats: Family Bathyergidae. In: Evolution of Subterranean Mammals at the Organismal and Molecular Levels. Ed. by E. Nevo and O. A. Reig. New York: Wiley Liss. Publ. pp. 97–128.
— (1991): Behaviour and ecology of the Family Bathyergidae. In: The Biology of the Naked Mole-rat. Chapter 3. Ed. by P. W. Sherman, J. U. M. Jarvis, and R. D. Alexander. Princeton: University Press.
Lighton, J. R. B. (1985): Minimum costs of transport and ventilatory patterns in three African beetles. Physiol. Zool. **58**, 390–399.
Lovegrove, B. G. (1986a): The metabolism of social subterranean rodents: adaptation to aridity. Oecologia (Berlin) **69**, 551–555.
— (1986b): Thermoregulation of the subterranean rodent genus *Bathyergus* (Bathyergidae). S. Afr. J. Zool. **21**, 283–288.
— (1987): Thermoregulation in the subterranean rodent *Georychus capensis* (Rodentia Bathyergidae). Physiol. Zool. **60**, 174–180.
McNab, B. K. (1979): The influence of body size on the energetics and distribution of fossorial and burrowing animals. Ecology **60**, 1010–1021.
— (1980): On estimating thermal conductances in endotherms. Physiol. Zool. **53**, 145–156.
Nevo, E. (1979): Adaptive convergence and divergence of subterranean mammals. Ann. Rev. Ecol. Syst. **10**, 269–308.
Nevo, E.; Ben-Shiomo, R.; Beiles, M.; Jarvis, J. U. M.; Hickman, G. C. (1987): Allozyme differentiation and systematics of the endemic subterranean mole-rats of South Africa (Rodentia, Bathyergidae). Biochem. Syst. Ecol. **15**, 489–502.
Nevo, E.; Capanna, E.; Corti, M.; Jarvis, J. U. M.; Hickman, G. C. (1986): Karyotype differentiation in the endemic subterranean mole-rats of South Africa (Rodentia, Bathyergidae). Z. Säugetierkunde **51**, 36–49.
Nevo, E.; Shkolnik, A. (1974): Adaptive metabolic variation of chromosome forms in mole-rats, *Spalax*. Experientia **30**, 724–726.
Rosenthal, C. M.; Bennett, N. C.; Jarvis, J. U. M. (1992): The changes in the dominance hierarchy over time of a complete field-captured colony of *Cryptomys hottentotus hottentotus*. J. Zool. (London) **228**, 205–225.
Sokal, R. R.; Rohlf, F. J. (1980): Biometry. New York: W. H. Freeman and Co.

Authors' addresses: Nigel C. Bennett and Gonzalo H. Aguilar, Department of Zoology, University of Cape Town, Rondebosch 7700, Cape Town; Peter J. Taylor, Durban Natural Science Museum, P.O. Box 4085, Durban, Republic of South Africa

Z. Säugetierkunde 58 (1993) 368–375

ISSN 0044-3468

The small mammal fauna in a hedge of north-eastern Bavaria

By S. Weisel and R. Brandl

Lehrstuhl Tierökologie I der Universität Bayreuth und Umweltforschungszentrum Leipzig-Halle GmbH, Bundesrepublik Deutschland

Receipt of Ms. 12. 10. 1992
Acceptance of Ms. 4. 12. 1992

Abstract

Investigated the small mammal fauna of a hedge in north-eastern Bavaria in 1988. Between March and December 5 species of rodents and 4 species of insectivores were caught by live trapping. Abundance and species diversity varied during the year with a peak in autumn. Compared to forests, rodent density was very high. The most abundant species was *Apodemus sylvaticus* (more than 300 individuals ha^{-1}). Captures per trap were highest in traps in dense vegetation and along the southern rim of the hedge. There was an extensive exchange of individuals between adjacent hedges.

Introduction

Hedges are well known elements within the agriculturally used landscapes of Europe. Hedges are not only important for the surrounding farmland, but provide habitats for a large variety of animals and plants and may serve as corridors between isolated woodlots (Hobbs 1992). Therefore hedges help to conserve wildlife within areas of industrialized agriculture. Despite this importance, the information about the fauna of hedges is quite limited (Pollard and Relton 1970; Rotter and Kneitz 1977; Tischler 1948; Turcek 1958; Zwölfer et al. 1984), especially concerning quantitative data about density and density fluctuations of a particular group. The present report describes species composition and abundance of a small mammal community in a hedge of north-eastern Bavaria.

Materials and methods

We investigated a hedge of an age of more than 30 years near Bayreuth (Bavaria, Upper Franconia). The hedge (HH in Tab. 1 and Fig. 4) covered approximately 2,500 m^2 (250 m long and 8 to 12 m wide) and was oriented from east to west. Dominant woody plant species within the hedge were oak (*Quercus robur*), ash-tree (*Sorbus aucuparia*) and maple (*Acer campestre*) trees, surrounded by thickets of sloe (*Prunus spinosa*), elder (*Sambucus nigra*), hawthorn (*Crataegus oxycanthes*) and wild rose (*Rosa* spec.). Several smaller hedges were found at different distances to this hedge, separated from each other by cultivated fields (Fig. 4). For a general description of hedges in northern Bavaria, see Reif (1983).

From the end of March to the beginning of December 1988, intensive trapping was conducted using 172 Longworth lifetraps (Chitty and Kempson 1949) arranged in a grid of 3 by 5 meters. A mixture of oat, fat and plant oil was provided as food and dry shavings served as insulation material. Excluding the period from 21. July to 4. August, traps were set every week for three consecutive days. No prebaiting preceded the trapping periods. Traps were checked every morning. All captured rodents were marked individually by ear tags using coloured plastic pearls attached to the ears by a nylon thread. For every individual weight, sex, reproductive condition, as well as the trap position in the hedge were recorded. Occasionally trapped insectivores were not marked individually.

According to the density of trees, bushes and different plant species in the undergrowth, the vegetation around each trap was classified as dense, intermediate or open.

To collect information on movements of small mammals between neighbouring hedges, additional traps were set in six adjacent hedges. The number of traps as well as the date, when the trapping period was started are given in table 1. Trapping was completed in all hedges at the beginning of December.

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5806-0368 $ 02.50/0

As all rodents were marked, we were able to analyse the data by capture-recapture models (Lebreton et al. 1992). We compiled capture histories for individuals by pooling all data of a month. We used the program JOLLY (Pollock et al. 1990) to estimate the population size within a month, the probability phi(i) that an animal present within hedge at month i will also be present at month i+1 as well as the probability B(i), the recruitment of new individuals to the hedge in the interval i to i+1 and alive at month i+1. For simplicity we call phi survival, but one should be aware that it includes two factors: mortality and emigration. B, called recruitment, includes reproduction and immigration.

Results

Table 1 shows the number of animals and diversity of small mammals trapped in the different hedges during the study period. For insectivores only presence or absence is indicated. The dominant rodent species was *A. sylvaticus*.

Between March and December the number of individuals as well as the species composition of the rodent community showed a prominent seasonal pattern (Fig. 1). While in the beginning of June only 3 animals were caught, a total of 77 individuals belonging to 4 different species (*A. sylvaticus, A. flavicollis, C. glareolus, M. agrestis*) was

Table 1. **Species and number of trapped individuals in our main hedge (HH) and 6 adjacent hedges (H1–H6; see also Fig. 4)**

For insectivores, * indicates the presence of a species. Numbers in parentheses refer to animals that were first marked in a different hedge. The start of the trapping period is also given in the table

	HH	H1	H2	H3	H4	H5	H6
Apodemus sylvaticus	147	25	36	12	5	2	3
	(19)	(8)	(14)		(3)	(6)	(1)
Clethrionomys glareolus	38	13	7	8			
	(5)	(2)	(4)				
Apodemus flavicollis	32	5	4		3		
	(4)	(5)				(1)	
Microtus agrestis	16				1		1
					(2)		
Mus musculus	4						
Sorex araneus	*	*					
Sorex minutus	*	*					
Crocidura leucodon	*						*
Talpa europaea	*						
Number of traps	172	10	10	5	3	3	3
Start of period	30.3	29.4	29.4	7.7	23.9	23.9	23.9

trapped during three consecutive days in late October. The seasonal pattern is somewhat different among species (Fig. 1). *A. sylvaticus* and *C. glareolus* were present between March and October. But *A. sylvaticus* had its population peak in October, whereas *C. glareolus* had its peak in August/September (Figs. 2, 3). In both species, population increase was mainly due to an increased recruitment and not an increased survival (Figs. 2, 3). Mean survival of *A. sylvaticus* is lower than survival of *C. glareolus* (0.47 versus 0.78). During the peak in autumn population size of *A. sylvaticus* within the main hedge was 77 individuals (density more than 300 individuals ha^{-1}). Maximum density of *C. glareolus* was 88 individuals ha^{-1}.

Similar to *A. sylvaticus, A. flavicollis* and *M. agrestis* had their population peaks in autumn. But these two species were never or only rarely trapped during summer (Fig. 1).

The total number of captures per trap was not uniform throughout the hedge, but was influenced by the location (northern hedge rim, hedge centre, southern hedge rim) and the

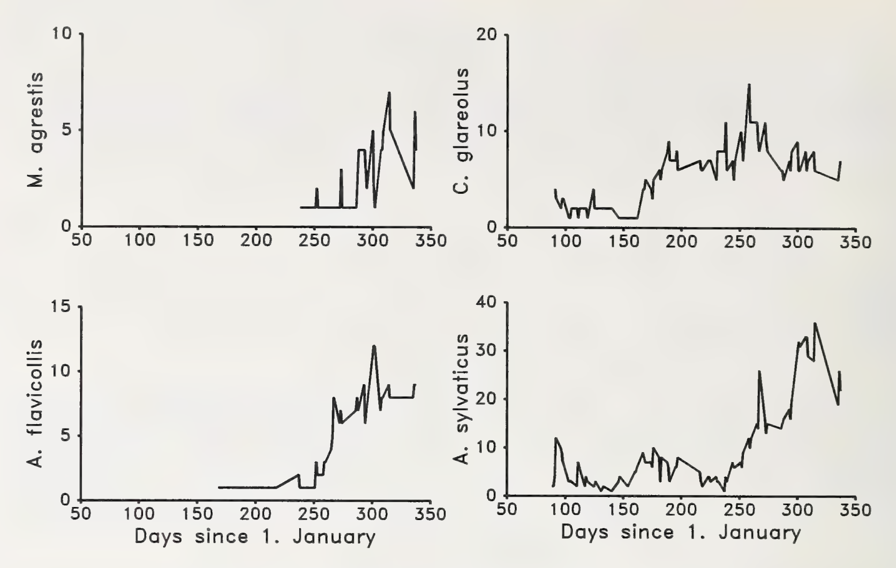


Fig. 1. Daily captures of the four most abundant rodent species

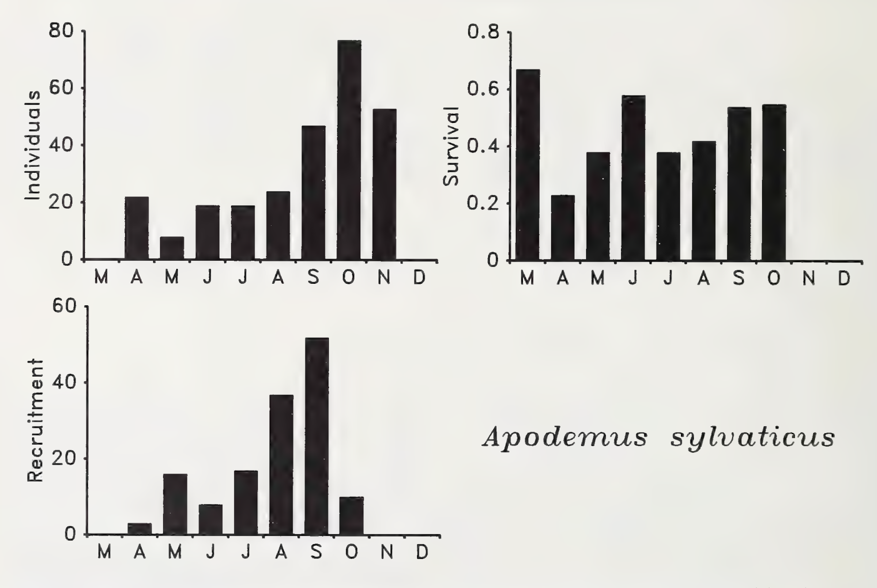


Fig. 2. Number of individuals, survival and recruitment of *A. sylvaticus* as estimated by the capture-recapture program JOLLY

vegetation cover (dense, intermediate, open). Table 2 presents the mean number of captures during the whole trapping period classified according to vegetation cover and position within the hedge. A two-way ANOVA revealed that both factors had significant influences on the effectiveness of a trap (vegetation cover $F = 9.9$; position $F = 34.6$; $P < 0.001$ in both cases). No significant interaction between vegetation cover around the trap and trap position was found ($F = 1.75$; $P = 0.14$).

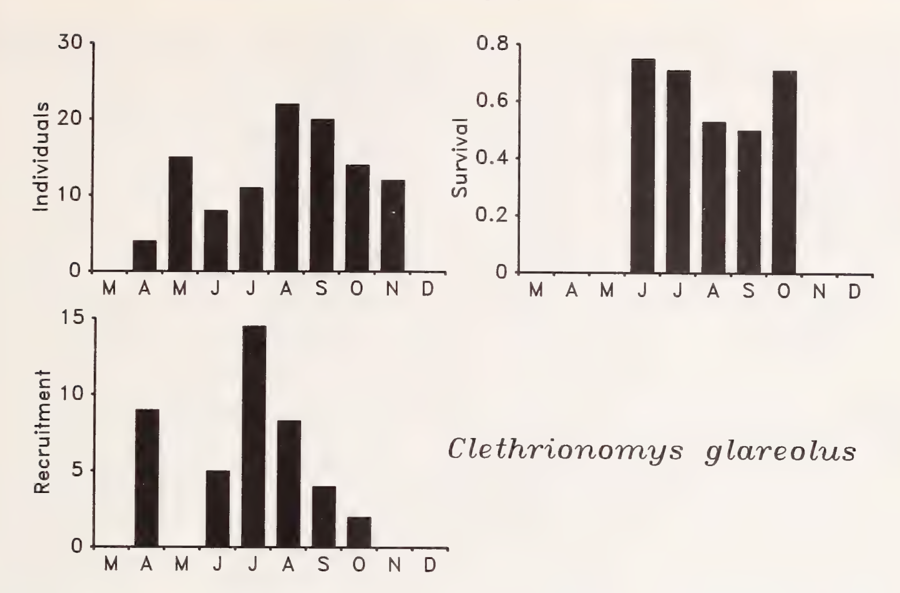


Fig. 3. Number of individuals, survival and recruitment of *C. glareolus* as estimated by the capture-recapture program JOLLY

Out of 362 marked individuals (237 marked in our main hedge and 125 marked in the other hedges), 62 (= 17 %) are known to have moved from the hedge, where they had first been captured, into one of the surrounding hedges (Fig. 4; Tabs. 3, 4). Proportions were not different among species ($Chi^2 = 1.4$; $P < 0.2$), with a significant preponderance of males in *A. sylvaticus* (Tab. 3). Average weights indicate that mainly adults are involved in these movements (Tab. 4). According to the trapping records, some individuals appeared at least in four neighbouring hedges. Only 2 of these individuals returned to the hedge, where they had been caught the first time.

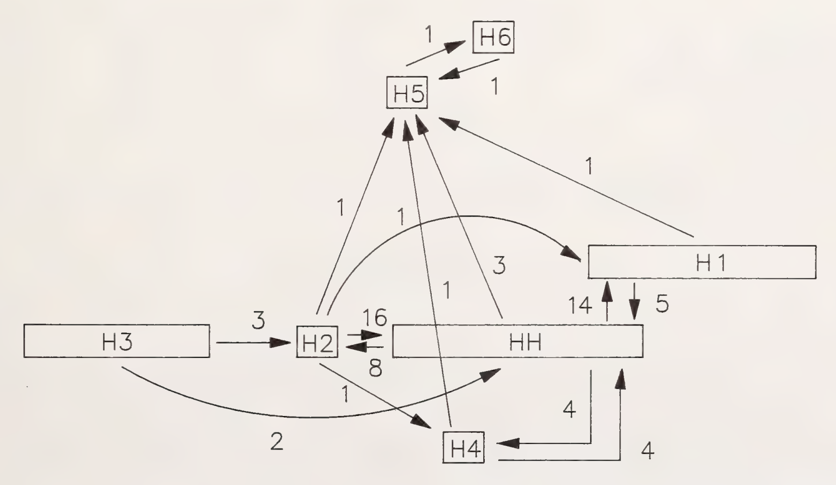


Fig. 4. Known movements of individuals among the hedges. The distance between H4 and H6 is 600 m

Table 2. **Mean number of captures per trap during the whole period classified according to trap location and vegetation cover**

	N_T	mean	SD
Trap location			
Northern rim	50	6.7	4.0
Centre	72	7.7	7.1
Southern rim	50	16.6	6.6
Vegetation cover			
Dense	82	13.0	8.1
Intermediate	72	7.2	6.0
Open	18	7.7	4.1

N_T = number of traps; SD = standard deviation.

Table 3. **Sex ratio of all marked individuals (I) and individuals which are known to have moved from the hedge, where they were first captured, to one of the surrounding hedges (II)**

		I	II	Chi²-Test
Apodemus sylvaticus	male	134	30	$Chi^2 = 5.8$
	female	96	9	$P = 0.016$
	% males	58	77	
Clethrionomys glareolus	male	38	8	$Chi^2 = 0.61$
	female	28	3	$P > 0.2$
	% males	58	73	
Apodemus flavicollis	male	20	5	$Chi^2 = 0.0$
	female	24	5	$P > 0.2$
	% males	45	50	

Table 4. **Mean weight (in g) of all marked individuals and of the individuals which are known to have moved of one of the surrounding hedges**

	N	Weight	SD	N	Weight	SD
Apodemus sylvaticus	230	18.5	4.7	39	22.1	4.5
Clethrionomys glareolus	66	17.4	4.0	11	20.2	3.8
Apodemus flavicollis	44	26.1	4.5	10	28.3	3.0
Microtus agrestis	18	18.3	4.7	2	22.5	0.7
Mus musculus	4	14.5	1.3			

N = sample size; SD = standard deviation.

Discussion

At present, only limited data on the small mammalian fauna of hedges are available. Besides the species caught during the present study, two additional rodents (*Muscardinus avellanarius, Glis glis*) and three insectivores (*Neomys fodiens, Neomys anomalus, Crocidura suaveolens*) were trapped in hedges at two localities in north-eastern Bavaria (Weisel unpubl.). However, similar results on the occurrence of small mammalian species in hedges were found by Tischler (1948) in northern Germany, Turcek (1958) in Slowenia, Pollard and Relton (1970) and Eldrige (1971) in England. Additional species listed by these authors are *Rattus norvegicus, Micromys minutus* and *Microtus arvalis*.

In addition to the biogeographic available species pool, hedge size, hedgerow management, type of the surrounding area (e.g. arable farmland, forest, wetland) and perhaps interspecific competition (Andrzejewski and Olszewski 1963; Boitani et al. 1985; Gliwicz 1984; Montgomery 1980) may influence density and species composition in a particular hedge. The different capture rates of traps indicate how small-scale microhabitat conditions affect the distribution of small mammals in hedgerows. Vegetation cover may be a reliable measure of shelter for foraging mammals, whereas the position within the hedge may be a measure of microclimatic conditions, because the southern hedge rim shows by far the highest activity of small mammals. We have, however, no ideas about the distribution of food within the hedge. Perhaps the southern hedge rim may have better food resources compared to the centre or northern rim of the hedge. Especially herbaceous plants were more common along the southern rim of the hedge.

Many reports note that the dynamics of small mammals are not only influenced by the reproductive output within the sampled plot, but also by adjacent agriculturally used areas (Kikkawa 1964; Pollard and Relton 1970). Especially the removal of the shelter by harvesting the fields may force small mammals to invade hedges from the adjacent fields, which may be one factor contributing to the density peak during autumn. *A. sylvaticus* is known to use cultivated fields as foraging and breeding sites during summer, but immigrate into nearby woodlands or hedges during autumn (Kikkawa 1964; Pollard and Relton 1970; Green 1979; Pelz 1979). Furthermore many plants produce their fruits and seeds during autumn and generate a good food resource within the hedge, which may attract mammals.

In addition to shelter and food resources, social interactions influence the dynamics of small mammal populations. Investigations by Watts (1969), Flowerdew (1974, 1985), Gurnell (1978) and Montgomery (1980) showed that intraspecific and density-dependent mechanisms influence populations of *A. sylvaticus*. Thereby, agonistic and aggressive behaviour of adult males from the previous year prevents the recruitment of subadults (either from the reproductive output within or from adjacent areas) into the breeding population in late spring and summer, thus keeping the total population stable until most of the old males have died at the end of the summer. Figure 1 seems to support this hypothesis: during summer there was a stable population and the recruitment of new individuals increased during August and September.

In summary beside reproduction within the hedge we have at least three further mutually non-exclusive explanations for the rodent peak during autumn: 1. invasions from agricultural areas; 2. local concentration at good food resources and 3. relaxation of intraspecific competition. It is a serious drawback of our study that we did not record information about the temporal change of food resources as well as the reproductive output within the hedge and adjacent areas to decrease the possible factors explaining the temporal pattern of rodent density within our hedge. One indication comes from the observation that the rodent density within our hedge was comparatively high. For example, Niethammer (1978) reported maximum densities of about 60 individuals ha^{-1} for *A. sylvaticus*. The high densities found within our hedge supports the idea of favourable food resources. One of the ultimate reasons for this observation may derive from an "edge effect". Compared to forests a hedge has much longer boundaries to the surrounding habitats with favourable growing conditions for a wide variety of plants. Furthermore, this edge effect may allow the coexistence of *A. sylvaticus* and *A. flavicollis* in autumn. We observed a positive correlation between both species (Fig. 1), whereas numerous papers report some competition between these two species (e.g. Schröpfer et al. 1984).

The average weight of all four rodent species indicates that mainly adults left the hedge, where they had first been caught. This finding contrasts with the age structure normally found among dispersing small mammals (Gipps 1985; Gains and McClenaghan 1980; Watts 1970; Wolten and Flowerdew 1985). However investigations of Kozakiewicz

and Jurasinska (1989) on the recolonization of a woodlot by *C. glareolus*, surrounded by a 30 m-wide stripe of meadow, revealed that the average weights and the proportion of sexually active animals of the colonizing animals were higher than in the control population from a nearby forest. For *A. sylvaticus* the preponderance of adult males that moved to adjacent hedgerows might reflect competition or aggression existing between the males within a hedge population (see also Gipps 1985; Montgomery and Gurnell 1985; Wolton 1985).

77 % of all movements (N = 48) were observed among hedges, located within 40 m to each other, thus being well within the range that individuals traversed inside our main hedge during one night (unpubl. obs.). The facts, however, that animals had to cross rather open area when leaving the hedge and that they did not return to their original hedge (with two exceptions), seem to classify these movements not only as excursions or sorties but as true dispersal (Wolton and Flowerdew 1985). Compared to investigations on the dispersal of rodents in woodlands (Watts 1969, 1970), fluctuations of individuals in hedges seems to be rather high. This underlines the possible importance of hedges as corridors for a faunal exchange between fragmented remnants within our landscapes.

Zusammenfassung

Die Kleinsäugerfauna einer Feldhecke in Nordostbayern

Zwischen März und Dezember 1988 wurde die Kleinsäugerfauna einer Feldhecke nahe Bayreuth in Oberfranken untersucht. Mittels Lebendfallen konnten 5 Nagerarten sowie 4 Insektenfresserarten nachgewiesen werden. Häufigkeit und Artenzahl der Nager zeigte im Herbst einen Höhepunkt. Die Dichte lag dabei über den Vergleichswerten in der Literatur. Die häufigste Art war *Apodemus sylvaticus* (mehr als 300 Individuen ha^{-1}). Die Attraktivität der Fallen war bei dichter Umgebungsvegetation sowie am Südrand der Hecke am besten. Zwischen benachbarten Hecken konnte ein reger Individuenaustausch festgestellt werden.

References

Andrzejewski, R.; Olszewski, J. (1963): Social behaviour and interspecific relations in *Apodemus flavicollis* (Melchior, 1834) and *Clethrionomys glareolus* (Schreber, 1780). Acta Theriol. **7**, 157–167.

Boitani, L.; Loy, A.; Molinari, P. (1985): Temporal and spatial displacement of two sympatric rodents (*Apodemus sylvaticus* and *Mus musculus*) in a Mediterranean coastal habitat. Oikos **45**, 246–252.

Chitty, D.; Kempson, D. A. (1949): Prebaiting small mammals and a new design of livetraps. Ecology **30**, 534–542.

Eldrige, J. (1971): Some observations on the dispersion of small mammals in hedgerows. J. Zool. (London) **165**, 530–534.

Flowerdew, J. R. (1974): Field and laboratory experiments on the social behaviour and population dynamics of the wood mouse (*Apodemus sylvaticus*). J. Anim. Ecol. **43**, 499–511.

Flowerdew, J. R. (1985): The population dynamics of wood mice and yellow-necked mice. Symp. zool. Soc. Lond. **55**, 315–338.

Gaines, M. S.; McClenaghan, L. R. Jr. (1980): Dispersal in small mammals. Ann. Rev. Ecol. Syst. **11**, 163–196.

Gipps, J. H. (1985): The behaviour of bank voles. Symp. zool. Soc. Lond. **55**, 61–87.

Gliwicz, J. (1984): Competition among forest rodents: effects of *Apodemus flavicollis* and *Clethrionomys glareolus* on *Apodemus sylvaticus*. Acta Zool. Fennica **172**, 57–60.

Green, R. (1979): The ecology of wood mice (*Apodemus sylvaticus*) on arable farmland. J. Zool. (London) **188**, 357–377.

Gurnell, J. (1978): Seasonal changes in numbers and male behavioural interaction in a population of wood mice, *Apodemus sylvaticus*. J. Anim. Ecol. **47**, 741–755.

Hobbs, R. J. (1992): The role of corridors in conservation: solution or bandwagon? TREE 7, 389–392.

Kikkawa, J. (1964): Movement, activity and distribution of the small rodents *Clethrionomys glareolus* and *Apodemus sylvaticus* in woodland. J. Anim. Ecol. **33**, 259–99.

Kozakiewicz, M.; Jurasinska, E. (1989): The role of habitat barriers in woodlot recolonization by small mammals. Holarctic Ecol. **12**, 106–111.

Lebreton, J.-D.; Burnham, K. P.; Clobert, J.; Anderson, D. R. (1992): Modelling survival and

testing biological hypotheses using marked animals: a unified approach with case studies. Ecol. Monographs **62**, 67–118.

MONTGOMERY, W. J. (1980): Spatial organization in sympatric populations of *Apodemus sylvaticus* and *A. flavicollis* (Rodentia: Muridae): J. Zool. (London) **192**, 379–401.

MONTGOMERY, W. J.; GURNELL, J. (1985): The behaviour of *Apodemus*. Symp. zool. Soc. Lond. **55**, 89–115.

NIETHAMMER, J. (1978): *Apodemus sylvaticus* (Linnaeus, 1758) – Waldmaus. In: Handbuch der Säugetiere Europas. Bd. 1. Ed. by J. NIETHAMMER, and F. KRAPP. Wiesbaden: Akademische Verlagsges. Pp. 337–358.

PELZ, H. J. (1979): Die Waldmaus, *Apodemus sylvaticus* L. auf Ackerflächen: Populationsdynamik, Saatschäden und Abwehrmöglichkeiten. Z. angew. Zool. **66**, 261–80.

POLLARD, E.; RELTON, J. (1970): Hedges 5. A study of small mammals in hedges and cultivated fields. J. appl. Ecol. **7**, 549–557.

POLLOCK, K. H.; NICHOLS, J. D.; BROWNIE, C.; HINES, J. E. (1990): Statistical inference for capture-recapture experiments. Wildlife Monographs **107**, 1–97.

REIF, A. (1983): Nordbayerische Heckengesellschaften. Hoppea, Denkschrift. Regensb. Bot. Ges. **41**, 3–204.

ROTTER, M.; KNEITZ, G. (1977): Die Fauna der Hecken und Feldgehölze und ihre Beziehung zur umgebenden Agrarlandschaft. Waldhygiene **12**, 1–82.

SCHRÖPFER, R.; FELDMANN, R.; VIERHAUS, H. (1984): Die Säugetiere Westfalens. Abh. Westf. Mus. Naturk. **46**, 1–393.

TISCHLER, W. (1948): Biozönotische Untersuchungen an Wallhecken Schleswig-Holsteins. Zool. Jb., Abt. Syst. **77**, 283–400.

TURCEK, F. (1958): Gehölze, Vögel und Säugetiere in einigen Strauch- und Buschstreifen in den Feldern. Biol. Proc **4**, 45–67.

WATTS, C. H. (1969): The regulation of wood mouse (*Apodemus sylvaticus*) numbers in Wytham Woods, Berkshire. J. Anim. Ecol. **38**, 285–304.

WATTS, C. H. (1970): Longdistance movements of bank voles and wood mice. J. Zool. (London) **161**, 247–256.

WOLTON, R. J. (1985): The ranging and nesting behaviour of wood mice. *Apodemus sylvaticus* (Rodentia: Muridae), as revealed by radiotracking. J. Zool. (London) **206**, 203–224.

WOLTON, R. J.; FLOWERDEW, J. R. (1985): Spatial distribution and movements of wood mice, yellow-necked mice and bank voles. Symp. zool. Soc. Lond. **55**, 249–75.

ZWÖLFER, H.; BAUER, G.; HEUSINGER, G.; STECHMANN, D. (1984): Die tierökologische Bewertung von Hecken. Akademie für Naturschutz und Landschaftspflege, Beiheft **3**, 1–555.

Authors' addresses: Dipl. Biol. SIEGFRIED WEISEL, Lehrstuhl Tierökologie I, Universität Bayreuth, Postfach 10 12 51, D-95412 Bayreuth, FRG; Dr. ROLAND BRANDL, Umweltforschungszentrum Leipzig-Halle GmbH, Sektion Ökosystemanalyse, Permoserstr. 15, D-04318 Leipzig, FRG

Z. Säugetierkunde 58 (1993) 376–377

ISSN 0044-3468

WISSENSCHAFTLICHE KURZMITTEILUNGEN

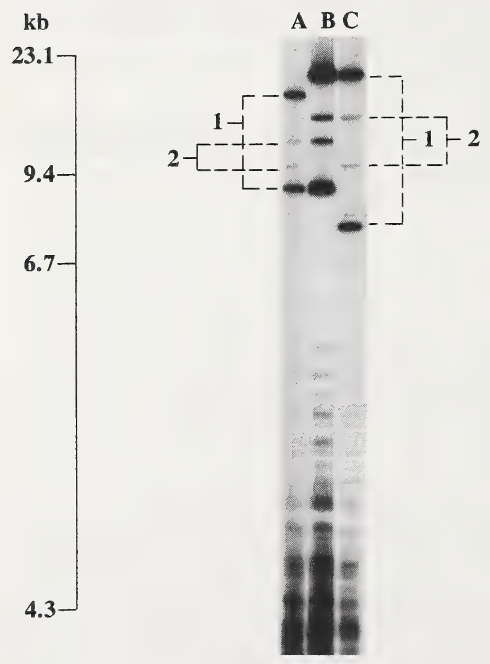
Monogamy in the Bat *Rhinolophus sedulus*?

By K.-G. Heller, R. Achmann, and Katrin Witt

Department of Zoology, University of Erlangen-Nürnberg, Erlangen

A large variety of mating systems has been observed in bats. While a few species live in harems, other form leks and some have promiscuous mating patterns or are assumed to establish monogamous relationships (for review see Bradbury 1977; McWilliam 1987a). Some of these mating systems are comparatively well studied, while solid evidence is lacking for most. The latter applies especially to the case of monogamous species. In several bat species it is known that parents stay together even when young are present (for review see Bradbury 1977), but in only one species (*Hipposideros beatus*) the existence of monogamous associations has been confirmed by long-term observations of marked animals for one breeding season (Brosset 1982). In this species males and females separate at the beginning of the next mating season and new pairs are formed (Brosset 1982).

Here we report observations on the lesser woolly horseshoe bat (*Rhinolophus sedulus* Andersen, 1905), a little known species restricted to peninsular Malaysia and Borneo. We observed it regularly (several times in 1984, 1989, 1992) roosting in road culverts alone or in pairs with and without young (Heller and Volleth 1989). Its close relative, the great woolly horseshoe bat, *Rhinolophus luctus*, is also known to roost singly or in pairs and was listed by Bradbury (1977) as probably monogamous.



DNA banding pattern of a family of *Rhinolophus sedulus* (A female, B young, C male). Assumed allelic fragment pairs are connected by dashed lines, 1 and 2 refer to the same locus

The bats were found close to the Ulu Gombak Field Studies Centre of the University of Malaya (3°20′ N, 101°45′ E) near Kuala Lumpur (for details of the study site see Heller and Volleth 1989). DNA from each animal in a single roosting group (male, female, young; forearm lengths 40, 40.5, 18.5 mm) was isolated from approximately 10 mg liver or pectoral-muscle tissue, which was cut into small pieces. DNA extraction, gel electrophoresis of Hinf I-restricted DNA and in-gel hybridization with the radiolabelled probe $(GATA)_4$ was performed as described previously (Achmann et al. 1992).

The DNA-profiles, which are different in all three individuals (Figure),

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5806-0376 $ 02.50/0

were remarkable in that they were sharply divided into two distinct patterns. In the low molecular weight range the multiband pattern of all three animals appeared to be almost identical. However, in the high molecular weight range the adults are clearly distinguished by a variable pattern of four bands in each animal. Only one of these bands may result from a DNA fragment of identical molecular weight in both adults (Figure). Two out of four bands of each adult's DNA-profile were characterized by high signal intensities, whereas the two other bands were considerably fainter. Since only one of each type is transmitted from each parent to the young, it is possible that two polymorphic loci were detected. In this case all animals would be considered heterozygous at both loci.

All bands of the young could be traced back to the female or the male, which suggested that both adults were the parents of the young. However, in the absence of more information on band-sharing or allele frequencies in *R. sedulus*, it is not possible to estimate exactly the probability of incorrect parentage. For the lactating female, maternity is surely not in question. For the putative father, however, the chance of incorrectly assigned parenthood depends primarly on the population allele frequencies of the detected bands. Given the two paternal-specific bands and a mean band-sharing coefficient (LANSMAN et al. 1981) of $x = 0,25$ (obtained from the comparison of both adults) the factor of $0.25^2 = 6.25\ \%$ would be a crude estimate of the probability that another male not closely related to the putative father actually fathered the young.

The DNA-profile of the young compared with that of the male and the female suggest that both adult animals were the parents of the young. The pairwise roosting behavior and these DNA profiles support the hypothesis of a stable male-female association after mating and even after the birth of the young, indicating a monogamous relationship. We have no information, however, on whether the observed pair remained together for more than one season as found in some harem breeding bats (e.g. McWILLIAM 1987b), or whether *R. sedulus* is seasonally monogamous as is *Hipposideros beatus* (BROSSET 1982).

Acknowledgements

We thank J. EPPLEN for providing the oligonucleotide probes, YONG HOI-SEN (University of Malaya) for enabling us to stay at the Ulu Gombak Field Studies Centre and O. von HELVERSEN, T. KUNZ, F. MAYER, M. VOLLETH and Y. WINTER for comments on the manuscript.

References

ACHMANN, R.; HELLER, K.-G.; EPPLEN, T. J. (1992): Last-male sperm precedence in the bushcricket *Poecilimon veluchianus* (Orthoptera, Tettigonioidea) demonstrated by DNA fingerprinting. Molecular Ecology **1**, 47–54.

BRADBURY, J. W. (1977): Social organization and communication. In: Biology of bats. Ed. by W. A. WIMSATT. New York, London: Academic Press. Vol. 3, 1–72.

BROSSET, A. (1982): Structure sociale du chiroptère *Hipposideros beatus*. Mammalia **46**, 3–9.

HELLER, K.-G.; VOLLETH, M. (1989): Fledermäuse aus Malaysia. 1. Beobachtungen zur Biologie, Morphologie und Taxonomie. Senckenbergiana biol. **69** (1988), 243–276.

LANSMAN, R. A.; SHADE, R. O.; SHAPIRO, J. F.; AVISE, J. C. (1988): The use of restriction endonucleases to measure mitochondrial DNA sequence relatedness in natural populations. J. Mol. Evol. **17**, 214–226.

McWILLIAM, A. N. (1987a): Territorial and pair behaviour of the African false vampire bat, *Cardioderma cor* (Chiroptera: Megadermatidae), in coastal Kenya. J. Zool. (London) **213**, 243–252.

McWILLIAM, A. N. (1987b): The reproduction and social biology of *Coleura afra* in a seasonal environment. In: Recent advances in the study of bats. Ed. by M. B. FENTON, P. RACEY, AND J. M. V. RAYNER. Cambridge: Cambridge Univ. Press. Pp. 324–350.

Authors' address: Dr. KLAUS-GERHARD HELLER, ROLAND ACHMANN and KATRIN WITT, Department of Zoology II, Staudtstr. 5, University of Erlangen-Nürnberg, D-91058 Erlangen, Germany

Z. Säugetierkunde 58 (1993) 378–380

ISSN 0044-3468

First records of the Malay civet, *Viverra tangalunga* Gray, 1832, on Seram with notes on the Seram bandicoot *Rhynchomeles prattorum* Thomas, 1920

By A. C. Kitchener, T. Clegg, N. M. J. Thompson, H. Wiik, and A. A. Macdonald

Department of Natural History, Royal Museum of Scotland and Department of Preclinical Veterinary Sciences, University of Edinburgh, UK

Receipt of Ms. 12. 10. 1992
Acceptance of Ms. 14. 6. 1993

The Malay civet (*Viverra tangalunga*) is widespread in South East Asia, having been recorded from peninsular Malaya, Palawan, Sumatra and neighbouring islands, Borneo, Sulawesi, Buru and Ambon (Honacki et al. 1982; Payne et al. 1985; van Strien 1986). In part its island distribution has arisen from human introductions as a consequence of the trade in live civets for their musk (Gijsels 1872). This parallels other deliberate introductions in Indonesia of rusa deer (*Cervus timorensis*) and wild pigs (*Sus scrofa, S. celebensis*) for meat (Groves 1976) and incidental introductions of several species of commensal rodents and the house shrew (*Suncus murinus*) (Laurie and Hill 1954).

On 3rd September 1990 an adult male Malay civet (National Museum of Scotland, Zoology, NMSZ no. 1990.129.1) was collected at 2,200 m near Wai Huhu (River Huhu) (3° 7′ S, 129° 28′ E) on the north side of Gunung Binaiya, central Seram, Maluku Province, Indonesia. This is an area of disturbed montane forest with a good understorey of tree ferns, ferns and bracken. It is used regularly by people from the village of Kanikeh (3° 6′ S, 129° 27′ E) as a camp-site during hunting trips. As a result considerable disturbance is caused by human hunters to this area in the provisioning of wood and other vegetation for fires and the building of temporary shelters. The following morning an adult female Malay civet (NMSZ 1990.129.2) was collected at the same site. The uterus contained three well-developed foetuses, two in the left horn and one in the right horn.

On 14th August 1991 another adult female Malay civet (NMSZ 1992.10.25) was collected during the night at the same locality, suggesting that this species is well established at this altitude. The uterus contained a single well-developed foetus in the right horn. Gut contents included insects (mostly crickets), unidentifiable plant matter and small mammal fur, which was probably from *Rattus exulans* and/or possibly *Suncus murinus*. Although carnivores generally avoid eating shrews because they are distasteful, small numbers are occasionally recorded in their stomachs and scats (see Kitchener 1991).

A juvenile male Malay civet (NMSZ 1992.10.26) was shot by local police on 25th August 1991 in the town of Wahai on the northern coast of Seram (2° 48′ S, 129° 28′ E), thereby confirming the presence of this species from sea-level to 2,200 m. Gut contents included invertebrates (crickets and centipedes), fruits and other plant matter. The stomach contents of both civets (NMSZ 1992.10.25–26) were similar to the food items found in the scats of Malay civets in Sarawak (Macdonald and Wise 1979). Predissection body weights and measurements of all civets collected on Seram are given in the table.

These results confirm recent suggestions that the Malay civet might be present on Seram (Ellen 1972). This is not surprising given the presence of this species on the neighbouring islands of Buru and Ambon (Honacki et al. 1982; van Strien 1986). However, it is also evident that the Malay civet has been on Seram for some considerable time and is not a recent introduction. In Seram this species is known by the Bahasa Indonesia word

U.S. Copyright Clearance Center Code Statement: 0044-3468/93/5806-0378 $ 02.50/0

Body measurements and weights of the Malay civet, *Viverra tangalunga*, on Seram, Indonesia

Register no.	Sex	HB (mm)	TL (mm)	HF (mm)	Body weight (kg)	Locality
1990.129.1	M	650	320	70	3.20	Wai Huhu
1990.129.2	F	670	290	95	3.80	Wai Huhu
1992.10.25	F	645	250	93	3.38	Wai Huhu
1992.10.26	M	435	230	83	1.25	Wahai

HB – head and body length; TL – tail length; HF – hind foot length.

"Musang", but the people of Kanikeh call it "Makulele" and consider it to be a common animal. These four specimens represent the first records of this species on Seram (Laurie and Hill 1954).

The palm civet (*Paradoxurus hermaphroditus*) is also recorded from Seram (Laurie and Hill 1954) and is known to local people as "Tupai" or "Tosia", although it was not recorded during fieldwork in 1990 and 1991. The palm civet is also known as "Tingalong", which bears a striking resemblance to "Tangalung", which is the Malay name for the Malay civet (Payne et al. 1985). However, it is possible that the name "Tingalong" is used for both species of civet on Seram, because people in Wahai referred to the young male Malay civet by this name.

Attempts were also made to discover any trace of the endemic bandicoot, *Rhynchomeles prattorum*, which has not been recorded since its discovery by the Pratt brothers in 1920 (Thomas 1920). Indeed, Archer (1984) believes that *Rhynchomeles* is completely extinct. In 80 trap nights in the study site described above and a lower one at 1,800 m altitude no bandicoots were caught. There was also no sign of bandicoot activity in and around the two study sites despite extensive searches.

There are three possible hypotheses to explain the absence of *Rhynchomeles*: 1. complete or local extinction caused by introduced predators including the Malay civet, 2. competition from other introduced mammals and 3. habitat disturbance caused by human activity.

The records of the Malay civet on Seram and its familiarity with local people suggest that it is a well-established member of the mammal fauna und that any decline in numbers of endemic mammals would have been expected to occur possibly hundreds of years ago when this species was actively traded (Gijsels 1872). Feral cats and dogs represent more competent predators, the latter having been present on Seram since about 3,000 years BP (Ellen 1993). Therefore, predation is unlikely to have caused a recent extinction of *Rhynchomeles*.

Only house shrews (*Suncus murinus*) and Polynesian rats (*Rattus exulans*) were caught during 340 trap nights using a variety of trap sizes ranging from Longworth small mammal traps to Tomahawk live traps up to 45 cm × 45 cm × 125 cm. The trapping success for both species (4 %) was similar to that recorded in similar habitat on Biliran Island in the Philippines (Heidemann et al. 1987). Although both these introduced species are normally commensal with humans (e.g. Laurie and Hill 1954; Lekagul and Mcneely 1977; Corbett 1978; Musser and Newcomb 1983), on Gunung Binaiya they are feral. Similar feral populations have been recorded on the islands of Biliran and Negros in the Philippines irrespective of the presence of endemic mammals (Heidemann et al. 1987). It seems likely that these introduced mammals have filled vacant niches on Seram rather than forcing out endemic mammals. This is supported by Musser and Newcomb (1983), who found that Polynesian rats were closely tied to human settlements in the rest of the Malayan region.

Conversations with people from villages on and around Gunung Binaiya suggest that the Seram bandicoot may still survive in the undisturbed montane forest on the Merkele

Ridge to the west of Kanikeh (Ellen 1972; Macdonald et al. 1993), despite claims that it is already extinct (Archer 1984). This suggests that habitat disturbance caused by human activities may be locally excluding *Rhynchomeles* and other endemic mammals.

Acknowledgements

We gratefully acknowledge the financial support of the Wellcome Trust, the Carnegie Trust for the Universities of Scotland, the National Museums of Scotland, the University of Edinburgh, the Royal Zoological Society of Scotland and the Balloch Trust. We thank Dr. Paul Chanin for the loan of mink traps. We are also very grateful to the many people too numerous to mention in Indonesia and Britain who made this fieldwork possible.

References

Archer, M. (1984): The Australian marsupial radiation. In: Vertebrate zoogeography and evolution in Australasia. Ed. by M. Archer and G. Clayton. Canberra: Hesperian Press. Pp. 633–808.
Corbet, G. B. (1978): The mammals of the Palaearctic region. London: British Museum (Nat. Hist.).
Ellen, R. F. (1972): The marsupial in Nuaulu ritual behaviour. Man **7**, 223–238.
Ellen, R. F. (1993): Human impact on the environment of Seram. In: Natural History of Seram. Ed. by I. D. Edwards, A. A. Macdonald and J. Proctor. Andover: Intercept Press. Pp. 191–206.
Gijsels, A. (1872): Grondig verhaal van Amboyna, 1621. Kroniekvan het Historisch Genootschap, Utrecht **27**, 348–394, 397–444, 450–494.
Groves, C. P. (1976): The origin of the mammalian fauna of Sulawesi (Celebes). Z. Säugetierkunde **41**, 201–216.
Heidemann, P. D.; Heaney, L. R.; Thomas, R. L.; Erickson, K. L. (1987): Patterns of faunal diversity and species abundance of non-volant mammals on Negros Island, Philippines. J. Mammalogy **68**, 884–888.
Honacki, J. H.; Kinman, K. E.; Koeppl, J. W. (1982): Mammal species of the world. Lawrence, Kansas: Allen Press.
Kitchener, A. (1991): The natural history of the wildcats. London: Helm.
Laurie, E. M. O.; Hill, J. E. (1954): List of the land mammals of New Guinea, Celebes and adjacent islands, 1758–1952. London: British Museum (Nat. Hist.).
Lekagul, B.; Mcneely, J. A. (1977): Mammals of Thailand. Bangkok: Kurusaphra Ladprao Press.
Macdonald, A. A.; Hill, J. E.; Boeadi; Cox, R. (1993): The mammals of Seram, with notes on their biology and local usage. In: Natural History of Seram. Ed. by I. D. Edwards, A. A. Macdonald, and J. Proctor. Andover: Intercept Press. Pp. 161–190.
Macdonald, D. W.; Wise, M. J. (1979): Notes on the behaviour of the Malay civet *Viverra tangalunga* Gray. Sarawak Museum Journal **48**, 295–299.
Musser, G. G.; Newcomb, S. C. (1983): Malaysian murids and the giant rat of Sumatra. Bull. Am. Mus. Nat. Hist. **174**, 327–598.
Payne, J.; Francis, C. M.; Phillips, K. (1985): A field guide to the mammals of Borneo. Kota Kinabalu: Sabah Society.
Strien, N. J. van (1986): Abbreviated checklist of the mammals of the Australasian Archipelago. Bogor: School Environ. Conserv. Managem. Pp. 1–91.
Thomas, O. (1920): On mammals from Seram. Ann. Mag. Nat. Hist. (Series 9) **6**, 422–431.

Authors' addresses: A. C. Kitchener, Department of Natural History, Royal Museum of Scotland, Edinburgh, EH1 1JF, UK; Tamsin Clegg, Linklaters and Paines, Barrington House, 59–67 Gresham Street, London, EC2V 7JA, UK; N. M. J. Thomson, H. Wiik, and A. A. Macdonald, Department of Preclinical Veterinary Sciences, The University of Edinburgh, Summerhall, Edinburgh, EH9 1QH, UK

Ausschreibung des FRITZ-FRANK-Preises
Förderpreis der Deutschen Gesellschaft für Säugetierkunde

Die Deutsche Gesellschaft für Säugetierkunde schreibt diesen Förderpreis in Höhe von DM 3000,– als Anerkennung für hervorragende wissenschaftliche Leistungen junger Forscher/innen aus.

Voraussetzung ist eine im Druck vorliegende Arbeit oder eine hervorragende Dissertation aus den Gebieten Phylogenie und Systematik, Verbreitung, Ethologie, Ökologie und Populationsbiologie der Säugetiere. Die Arbeit muß in den drei vorausgehenden Kalenderjahren erschienen oder als Dissertation begutachtet worden sein. Die Bewerber/innen dürfen beim Erscheinen der Arbeit bzw. bei ihrer Promotion nicht älter als 33 Jahre sein.

Bewerbungen der Vorschläge erbitten wir an die Geschäftsstelle der Gesellschaft, Prof. Dr. H. ERKERT, Zoologisches Institut der Universität, Auf der Morgenstelle 28, D 72076 Tübingen, unter Beifügung von fünf Sonderdrucken bzw. Kopien der Dissertation bis zum 31. 3. 1994.

Der Jury gehören Wissenschaftler verschiedener Universitäten oder Museen und Mitglieder der Gesellschaft an.

Der Preis wird bei der Eröffnung der Jahresversammlung der Gesellschaft in Wien (25.–29. 9. 1994) überreicht.

Über die Mitgliederversammlung der Deutschen Gesellschaft für Säugetierkunde e. V. am 27. September 1993 im Hörsaal N5 der Universität Tübingen

Der 1. Vorsitzende, Herr SCHMIDT, eröffnet die Versammlung um 17 Uhr bei Anwesenheit von 62 Mitgliedern.

1. Die Tagesordnung wird mit Ergänzungen angenommen.
2. Der Geschäftsführer, Herr ERKERT, verliest den Bericht über das Jahr 1992. Auf Einladung von Herrn RIETSCHEL fand die 67. Hauptversammlung der Gesellschaft vom 20.–25. September 1992 in Karlsruhe statt. Schwerpunktthemen waren „Paläontologie der Säugetiere", „Sozialverhalten der Säugetiere" sowie „Biologie der Chiropteren". Mit 38 Vorträgen, 37 Postern und rund 200 Teilnehmern war die Veranstaltung ein Erfolg. Der FRITZ-FRANK-Preis der DGS wurde an Frau KALKO für ihre Arbeit „Das Echoortungs- und Jagdverhalten von drei europäischen Zwergfledermausarten" vergeben. Vier Poster wurden mit Buchpreisen bedacht, die der Verlag Paul Parey gestiftet hatte. Im Anschluß an die Tagung fand ein Workshop zur Situation des Fledermausschutzes in Deutschland statt. Dabei wurde die Bildung einer Koordinationsgruppe „Fledermausschutz in Deutschland" unter dem Dach der DGS beschlossen. Herr ERKERT dankt den Veranstaltern, Herrn RIETSCHEL, Frau BRAUN und besonders Herrn FLÖSSER, für die Ausrichtung der erfolgreichen Tagung.
   Im Berichtsjahr erschien der 57. Band der „Zeitschrift für Säugetierkunde" in sechs Heften mit insgesamt 384 Seiten; den beiden Schriftleitern und aktiven Herausgebern wird gedankt. Die Mitgliederzahl hat sich bis Ende 1992 auf 620 erhöht.
   Durch den Tod verlor die Gesellschaft folgende Mitglieder:
   Dr. LUTZ BRIEDERMANN, Niederfinow,
   Prof. Dr. HEINZ TOBIEN, Ingelheim.
3. Herr ERKERT erläutert den von Frau KÜHNRICH abgefaßten detaillierten Kassenbericht.

4. Die Herren BOHLKEN und SCHLIEMANN haben die Kontounterlagen der Gesellschaft in Hamburg geprüft und für korrekt befunden.
5. Die Anträge auf Entlastung der Schatzmeisterin und des Vorstandes werden bei Enthaltung des Vorstandes angenommen.
6. Die Herren BOHLKEN und SCHLIEMANN werden bei einer Enthaltung als Kassenprüfer für das Geschäftsjahr 1993 gewählt. Beide sind mit der Wahl einverstanden.
7. Der Vorstand schlägt eine Erhöhung der Mitgliedsbeiträge für 1994 für Vollmitglieder von 95,– auf 100,– DM und für Studenten, deren Beitrag seit 1983 unverändert ist, von 60,– auf 65,– DM vor. Als Gründe werden erhöhte Portokosten ab 1993 und der Wegfall von Vergünstigungen durch den Verlag Paul Parey genannt. Nach reger Diskussion, in der sowohl gegen als auch für eine deutlich stärkere Erhöhung plädiert wird, stimmt die Mehrheit der Mitglieder (52 Ja, 3 Nein, 7 Enthaltungen) dem Antrag zu.
8. Die Mitgliederversammlung nimmt die Einladung von Frau SPITZENBERGER an, die 68. Jahresversammlung vom 25.–29. September 1994 in Wien abzuhalten. Schwerpunktthemen werden „Akustische Kommunikation und Gehör“, „Biologie der Insectivora“ und ein weiteres, noch von Frau SPITZENBERGER auszuwählendes Thema sein. Per Akklamation wird die Einladung von Herrn FISCHER, 1995 in Göttingen zu tagen, angenommen.
9. In zweiter Lesung werden die allen Mitgliedern vorliegenden Satzungsänderungen im Detail besprochen und einzeln zur Abstimmung gestellt. Betroffen sind die §§ 2, 3, 7c, 10, 11, 12, 13, 17 (gestrichen), 18 (künftig 17) und 19 (künftig 18). Alle Änderungen werden mit erforderlicher Mehrheit angenommen. Die Satzungsänderungen insgesamt werden anschließend einstimmig wie niedergelegt beschlossen.
10. a. Kommissionen und Arbeitsgruppen der DGS berichten über ihre Tätigkeit. Von der Tierschutz-Kommission liegt kein Bericht vor. Dies wird allgemein kritisiert, da entscheidende Gesetzesänderungen anstehen. Einstimmig wird der Antrag gebilligt, daß die Kommission bei der nächsten Tagung in Wien ein Konzept vorlegen und ihre Arbeitsfähigkeit belegen soll.
    b. Herr BOTHE berichtet, daß die „Arbeitsgruppe Bisam“ vom 4.–6. April 1993 mit rund 50 Teilnehmern in Braunschweig getagt hat. Die DGS hat das Treffen bezuschußt. Herr ERKERT regt an, Arbeitstreffen, wenn möglich, mit Jahrestagungen zu koordinieren.
    c. Herr SCHMIDT berichtet über die Arbeit der „Koordinationsgruppe Fledermausschutz“. Vom 22.–25. Juli 1994 wird auf Einladung von Herrn SCHMIDT in Bonn ein Symposium zum Thema „Current problems of bat protection in Central and Eastern Europe“ stattfinden.
    d. Herr HEIDECKE beabsichtigt, eine „Arbeitsgruppe Biber“ zu gründen. Die Mitglieder begrüßen diesen Plan.
    e. Herr GANSLOSSER berichtet über den Stand der im Vorjahr angeregten „Arbeitsgruppe Tiergarten-Biologie“.
    f. Herr SCHRÖPFER berichtet über die aktuellen Probleme im Hinblick auf Tier- und Artenschutzämter und schlägt eine Arbeitsgruppe über nationale Artenschutzprobleme vor. Die Mitglieder bitten Herrn SCHRÖPFER, ein Konzept auszuarbeiten, welches 1994 in Wien beraten werden soll.
    g. Herr KRUSKA fragt, wer darüber bestimmt, welche Veranstaltungen unter dem Emblem der Gesellschaft stattfinden. Zunächst sollen einige Erfahrungen gesammelt und dann über ein verbindliches Verfahren beraten werden.
    h. Herr PELZ fragt nach der Umsetzung der Vorschläge der Reformkommission. Herr HUTTERER antwortet, daß sich die Vorschläge bisher in den Satzungsänderungen und in den Arbeitsgruppen niedergeschlagen haben.
    j. Frau MÜNCH kann Interessenten Informationen über die internationale „Hörnchen-Gruppe“ geben.

11. a. Herr SCHMIDT informiert die Mitglieder über die Veränderungen im Verlag Paul Parey und die möglichen Folgen für die „Zeitschrift für Säugetierkunde“.
    b. Auf Nachfrage von Herrn HUTTERER herrscht Einigkeit darüber, daß keine Änderungen am Logo der Gesellschaft ohne Zustimmung der Mitgliederversammlung vorgenommen werden können.
    c. Die Mitgliedschaft der DGS in der Union Deutscher Biologischer Fachverbände hat bisher keine erkennbaren Vorteile gezeitigt. Es soll noch ein Jahr abgewartet werden.

Die Sitzung endet um 19.55 Uhr.

Prof. Dr. U. SCHMIDT	Prof. Dr. H. ERKERT	Dr. R. HUTTERER
1. Vorsitzender	Geschäftsführer	Beisitzer

BUCHBESPRECHUNG

BURNS, J. J.; MONTAGUE, J. J.; COWLES, C. J. (eds.): **The Bowhead Whale.** Lawrence, Kansas: Society for Marine Mammalogy, Spec. Publ. No. 2, 1993. 787 pp., numerous figures and tables. US $ 75,–. ISBN 0-935868-62-3

This outstanding book deals with *Balaena mysticetus,* the "bowhead", "Greenland", "Arctic", "polar" or "right whale". It is authored by 37 contributors and represents the result of seven years of preparation. The present reviewer can only hope that the book is not a voluminous "obituary". On page 548 W. G. ROSS writes: "No one can confidently say that the stocks ... will survive." The minimum total estimate of the population of this species for the time before commercial whaling in the early 16th century amounts to about 50 000 bowhead whales in the Bering and Okhotsk Seas, Spitsbergen, Davis Strait, Hudson Bay (WOODBY and BOTKIN, p. 404). The present-day stocks amount to about 8000 animals, of which 7500 live in the Bering Sea (ZEH et al., p. 480).

In an introductory chapter MONTAGUE introduces programs of research, US legislation and policy and study projects dealing with bowhead whales. NIEBAUER and SCHELL introduce the reader to the physical environment of the Bering Sea. Of general interest is a detailed chapter by MCLOED et al. dealing with evolutionary relationships, paleontology and systematics of the species. A chapter by HALDIMAN and TARPLEY compiles information on anatomy and physiology. Although the chapter comprises 85 pages, only very little physiological information can be presented. In spite of technical difficulties related to visual observations and acoustic records with the help of hydrophones, WÜRSING and CLARK are able to give an informative account of bowhead behavior. LOWRY presents information on the bowhead food, which consists mostly of copepods and euphausiids. His chapter addresses the still unanswered question why the Bering Sea stock periodically leaves highly productive areas and migrates for 3000 km into less productive waters farther north.

For reasons of conservation and to understand population dynamics, an account of reproductive biology as presented by KOSKI et al. is essential. It is interesting to note that average females of *Balaena mysticetus* become sexually mature when they attain a body length of 14.2 m. On the other hand, males already mature at a total length between 12 to 13 m. In Barrow, Alaska, PHILO et al. were able to study morbidity and mortality of bowhead whales. Mortality as a result of Eskimo subsistence hunting, as well as parasitic infections, wounds, ice entrapment and other factors are documented.

After the species' distribution and migratory movements are discussed by MOORE AND REEVES, two chapters deal with bowhead stocks before the beginning of commercial whaling (WOODBY and BOTKIN) as compared to the current population size (ZEH et al.). The comparison of data is tragical. For example, before commercial whaling a minimum of 24 000 animals lived in the waters around Spitsbergen. Human activities have been so "effective" that today's number lies "in the tens"! The picture becomes even more gloomy when the results of feeding and especially growth intensity are considered, as indicated by measurements with stable isotopes: Bowheads grow very slowly and reach sexual maturity at an age of about 20 years (SCHELL and SAUPE)!

Historical aspects of animal numbers are considered in the three following chapters: Commercial whaling in the North Atlantic (ROSS), the North Pacific (BOCKSTOCE and BURNS) and modern subsistence whaling by Eskimos (STOKER and KRUPNIK) are discussed. It is very probable that hunting by North American aboriginal people influences the bowhead stock negatively. RICHARDSON and MALME discuss the influence of man-made noise (e.g., oil-drilling, ships, aircraft), and BRATTON et al. deal with potential effects of chemical contaminants on health and survival of this species.

In an epilogue BURNS emphasizes three points, which he considers important future research needs: a. The role of fermentation in digestion and energetics of bowhead whales. b. Determination of bowhead distribution in ice-covered waters with the help of acoustical monitoring. c. Integration, synthesis, and assessment of environmental and biological data about bowhead whales and their habitat.

Each chapter is followed by a detailed list of references. These as well as two indices, a geographic and a general one, make the impressive wealth of information contained in this monograph on a fascinating mammal readily accessible.

P. LANGER, Gießen



Erscheinungsweise und Bezugspreis 1993: 6 Hefte bilden einen Band. Jahresabonnement Inland: DM 378,– zuzüglich DM 13,80 Versandkosten; Jahresabonnement Österreich: öS 2940,– zuzüglich öS 140,– Versandkosten; Jahresabonnement Schweiz: sfr 364,– zuzüglich sfr 17,50 Versandkosten; Jahresabonnement EG-Binnenmarkt-Länder mit USt-ID-Nr.: DM 354,– zuzüglich DM 16,82 Versandkosten; Jahresabonnement EG-Binnenmarkt-Länder ohne USt-ID-Nr. und Drittländer: DM 378,– zuzüglich DM 18,– Versandkosten. Das Abonnement wird zum Jahresanfang berechnet und zur Zahlung fällig. Es verlängert sich stillschweigend, wenn nicht spätestens am 15. November eine Abbestellung im Verlag vorliegt. Die Zeitschrift kann bei jeder Buchhandlung oder bei der Verlagsbuchhandlung Paul Parey GmbH & Co. KG, Spitalerstraße 12, D-20095 Hamburg, Bundesrepublik Deutschland, bestellt werden. Die Mitglieder der „Deutschen Gesellschaft für Säugetierkunde“ erhalten die Zeitschrift unberechnet im Rahmen des Mitgliedsbeitrages.

Z. Säugetierkunde 58 (1993) 6, 321–384

Mit dem Bandinhaltsverzeichnis

Pferdefütterung

Von Prof. Dr. Dr. h. c. Helmut Meyer, Direktor des Instituts für Tierernährung der Tierärztlichen Hochschule Hannover.
2., verbesserte und erweiterte Auflage. 1992. 223 Seiten mit 34 Abbildungen und 97 Tabellen. Gebunden DM 39,80
ISBN 3-489-64732-7

Die zweite Auflage seines erfolgreichen Buches „Pferdefütterung" hat der Autor in allen Kapiteln entsprechend den rasch zunehmenden wissenschaftlichen Erkenntnissen auf diesem Gebiet gründlich überarbeitet und dem neuesten Wissensstand angepaßt. Zusätzlich konnten u. a. Fragen über Haltung, Rassen, Leistungen und Körperzusammensetzung eingehender behandelt werden. Auch einigen speziellen Problemen wie Fütterung der Leistungspferde, Beziehungen zwischen Fütterung und Krankheit oder Ernährung kranker Pferde wurde mehr Raum gegeben. Mit neuen praxisreifen Erkenntnissen erfüllt die Neuauflage alle Ansprüche sowohl von Pferdehaltern mit ihren unterschiedlichen Intentionen, als auch von Tierärzten, Studierenden der Veterinärmedizin und allen an der Pferdeernährung Interessierten.

Aus einer Besprechung der ersten Auflage:

„Wem dieses Buch von Professor Meyer noch unbekannt ist, der sollte schnellstens diese wichtige Fütterungslehre anschaffen. Neben den anatomischen und physiolo-gischen Grundlagen wird sehr ausführlich auf den Bedarf und die Fütterungspraxis vom extensiv gehaltenen Pony bis hin zum Hochleistungspferd eingegangen."

Reiterjournal

Preis: Stand 1. Januar 1992



Berlin und Hamburg






SMITHSONIAN INSTITUTION LIBRARIES
SMITHSONIAN INSTITUTION WASHINGTON, D.C.


SMITHSONIAN INSTITUTION LIBRARIES
3 9088 00953 1161